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BULLETIN
OF THE
TORREY BOTANICAL CLUB

VOLUME 67 DECEMBER, 1940 NUMBER 9

THE EMBRYOGENY OF TORREYA, WITH A NOTE ON AUSTROTAXUS

J. T. BUCHHOLZ

(WITH FORTY-FOUR FIGURES)

INTRODUCTION

Several morphological investigations of *Torreya* (Tumion) have been published, but the embryogeny, except for the proembryo, still remains to be described. Strasburger (18) described the structures found in the longitudinal sections of a pair of the ovules of *T. nucifera* (L.) Seib. & Zucc. at the time of pollination. Miss Robertson, now Mrs. Agnes Arber (12, 13, 14), has given us, in a series of three papers, all that is known concerning the special morphology of *T. californica* Torrey, which included no mention of the events in the enlargement of the ovule and the maturity of the seed in the subseqent season. Coulter and Land (5) have given similar details for *T. taxifolia* Arnott. This work included the development of the proembryo, ovule, and seed in the season after fertilization. None of the remaining three species has been investigated. Since the accounts of these two species differed somewhat with respect to the size and structure of the female gametophytes and the number of archegonia, it is surprising that no one has subjected these, or any of the other species of *Torreya*, to additional investigation.

When these accounts are compared, one finds that the male gametophytes differ considerably in their relative stages of development near the time of fertilization. Miss Robertson's figures seem to show that at the time when the female gametophyte of *T. californica* is cellular and has its archegonia showing neck cells the pollen tube has only grown about half-way through the nucellus. For *T. taxifolia*, on the other hand, Coulter and Land have shown a figure in which the pollen tube has grown the full distance through the nucellus and is in contact with the female gametophyte while the latter is still in the free-nuclear stage of development. In other words, in *T. californica* the female gametophyte is precocious in development, while in *T. taxifolia* it appears that the male gametophyte is precocious.

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It was pointed out by Coulter and Land (5) that at the time of fertilization the female gametophyte of *T. taxifolia* consists of only 400 or more cells. It is, therefore, very small, only about 200×300 μ (by error given as 20×30 μ), which is somewhat smaller than *Taxus*, and very much smaller than either *Austrotaxus* (16) or *Cephalotaxus* (1, 4) at the time of fertilization, the latter being nearly 12 mm. long in this stage. It is well known that the female gametophyte of *Taxus* enlarges considerably after fertilization, but much less than *Torreya*, which has, in addition, the infolded and corrugated female gametophyte usually described (5) as a "ruminating endosperm."

Another remarkable feature is the small size of the archegonia. These are only 70×100 μ at the time of fertilization of *T. taxifolia* and there is usually only one. According to Miss Robertson's drawings the archegonia of *T. californica* are much larger, 85–90 μ × 180–250 μ at the time of fertilization. The number of archegonia is usually 3 and ranges between 2 and 5. However, these sizes given for the archegonia show that they are no smaller than those of *Taxus* (7, 8) at the time of fertilization, but they are only about half the size of those of *Austrotaxus* (15) and *Cephalotaxus* (4). Miss Robertson's drawings show that the size of the female gametophyte, at a stage before fertilization with half-grown pollen tube, are 420×625 μ and, in a later stage with proembryos, they are 480×1100 μ. The female gametophyte is, therefore larger in *T. californica* than in *T. taxifolia*.

Other differences have been recorded in the archegonia. Miss Robertson (13) found four or more neck cells (she shows one instance with 6 neck cells) and mentioned the differentiation of jacket cells. Coulter and Land (5) found only two neck cells, which usually disintegrate while in intimate contact with the pollen tube long before fertilization, and they recorded no specially differentiated archegonial jacket. The ventral canal nucleus is not formed in either species, though one mitotic figure which may represent the central cell nucleus in division was observed in *T. californica*. These differences in the female gametophytes all indicate that *T. californica* is the more primitive species and *T. taxifolia* is advanced with respect to the gametophytes near fertilization. The latter species has lost many gametophytic features which are found in other conifers and are still present in *T. californica*. Pilger (11) in his monographic treatment of the taxonomy of this group places *T. nucifera* as the most primitive species and considers *T. Fargesii* Franch., *T. taxifolia*, and *T. californica* as more advanced.

MATERIALS AND METHODS

The material which the writer has obtained for a study of the embryogeny came from several sources. Material of *T. nucifera* was obtained from the New York Botanical Garden in several stages of development and in different

years, no two of them in sequence. The stages before fertilization were obtained late in August, fertilization occurred in the last two weeks of September, and proembryos were found in all subsequent collections. However, a long dormant period ensues, so that there is no great change in the stage of development of the embryo from October until May or June of the following year. The ovules which enlarge in the spring were fertilized in the preceding September.

Several embryos of *T. californica* were obtained in 1936 from specimens found in cultivation at Golden Gate Park in San Francisco and later stages from Yosemite National Park near El Portal entrance. Through the kindness of Professor W. J. G. Land, I have received a series of microscopic slides, showing the morphology and embryogeny, which came from the Coulter and Land investigation, with permisson to include them in my investigation. This material of *T. taxifolia* included gametophytes before fertilization, proembryo stages similar to those described and figured by Coulter and Land (1904), and also several later stages, all of which had been sectioned. From these materials of three species the writer is able to present a general outline of the embryogeny of this genus. There are, no doubt, many important details concerning gametophytes and embryos which have been overlooked in this general survey.

The ovules of *T. nucifera* in fertilization stages were imbedded and sectioned by the usual methods after the scales had been removed by dissection under a binocular microscope. Preliminary dissection is necessary, since the scales which cover the ovules prevent a rapid penetration of the fixative and are difficult to cut. The ovules in the enlarged stages of the following season of both *T. nucifera* and *T. californica* were dissected by the methods described elsewhere (2), while those of *T. taxifolia*, which had already been sectioned, were delineated from the sections.

OBSERVATIONS

Torreya nucifera. Pollination had been very good, so that few ovules with healthy female gametophytes were without one or more pollen tubes. However, in 10 of 50 ovules (up to fertilization stage) one or more pollen tubes were observed with the entire absence of female gametophytes. In these the male gametophytes appeared to be normal; a month later such pollen tubes were found to be undergoing disintegration.

Figure 1 shows two archegonia of *T. nucifera* as found in the last week in August shortly before fertilization. The neck cells of the archegonia are still clearly visible and though crowded and slightly displaced in the archegonium at the right, they have not been digested by the action of the tip of the pollen tube, which, according to Coulter and Land (5), appears to arrive much earlier in *T. taxifolia* and destroys the neck cells. Many other

archegonia were observed with neck cells, including the ones shown in figures 5, 6, and 12. The number of neck cells in *T. nucifera* is usually 4 and ranges from 2 to 8. Of 42 archegonia in which the neck cells were counted, 5 had only 2, 2 had 2 or 3, 6 had 3, 1 had 3 or 4, 20 had 4, 2 had 5, 5 had 6, and 1 had 8 neck cells. These were always situated in the same plane or tier. The female gametophyte has a mean width of 260 μ and a mean length of 355 μ about a week before fertilization, has increased to 300 × 410 μ at fertilization and increases slightly during the following month up to the stage of winter dormancy.

The archegonia are usually 3 in number; only two may usually be observed in the same section. One doubtful case may have had only a single archegonium.

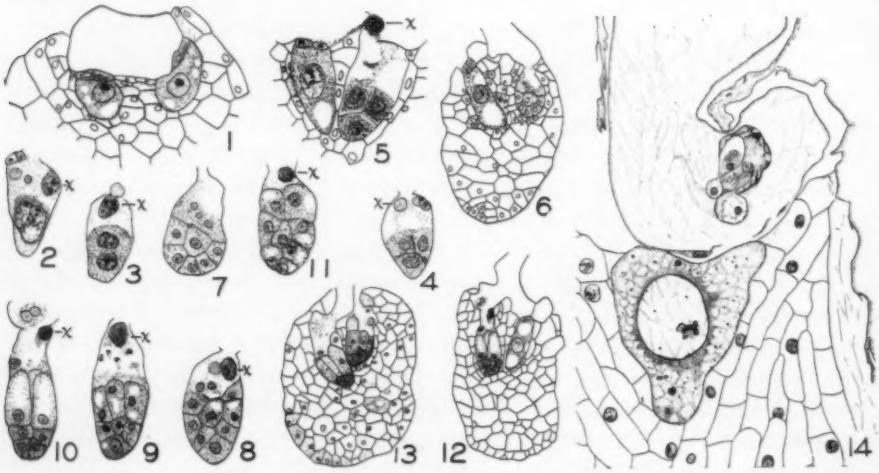


FIG. 1. Tip of female gametophyte of *T. nucifera* about September 1, before fertilization, showing two archegonia in contact with end of pollen tube. × 110. FIG. 2. Archegonium in fertilization. Male nucleus is in contact with egg nucleus with abandoned cytoplasm of male cells at *x* above, also the nucleus of smaller male cell. × 110. FIG. 3. Archegonium with proembryo in 2-nucleate stage, the abandoned male cytoplasm and smaller male nucleus showing in neck. × 110. FIG. 4. Proembryo with 4-nucleate stage, cell walls beginning to form. × 110. FIG. 5. Two adjacent archegonia, the one at left still unfertilized, the other with 4-celled proembryo, also shows the abandoned male cytoplasm *x* above neck. × 120. FIG. 6. Female gametophyte showing 2 archegonia, the one at right with proembryo. × 55. FIG. 7. Proembryo of figure 6, 10–12 celled stage; nuclei above proembryo may be smaller male nucleus, stalk, and tube nucleus. × 120. FIG. 8. 12-celled proembryo showing smaller male nucleus beside abandoned male cytoplasm, also two other nuclei which may have been derived from pollen tube. × 110. FIG. 9. A 12-celled proembryo with prosuspensors, beginning to elongate. Abandoned male cytoplasm above. × 110. FIG. 10. Similar proembryo showing elongation of prosuspensor, also male cytoplasm *x* and 3 nuclei. × 110. FIG. 11. Proembryo of 16–18 cells. × 110. FIG. 12. Section of gametophyte containing embryo of figure 10. × 55. FIG. 13. Section of female gametophyte with two proembryos resulting from the fertilization of two archegonia. × 55. FIG. 14. *T. taxifolia* showing relation of gametophytes at fertilization. In the pollen tube above at the right, the male nuclei are being discharged from the male cells. × 285.

In a count of 32 ovules with healthy female gametophytes before or at fertilization, 7 had only 2, 16 had 3, 8 had 4, and 1 had 5 archegonia. The mean dimensions of 32 young archegonia were ($49.3 \times 99.6\ \mu$) very nearly $50 \times 100\ \mu$. Archegonia in fertilization and early proembryo stages were $58 \times 120\ \mu$ (mean of 45 archegonia). Among those containing proembryos in which the neck region of the archegonia was more or less indefinite, the mean dimensions obtained from 24 were $74.5 \times 111\ \mu$. In many respects at the time of fertilization *T. nucifera* resembles *T. taxifolia* only in the small size of the archegonia, otherwise with respect to plurality of archegonia and neck cells it resembles *T. californica* much more closely, and in the size of female gametophytes it is intermediate.

No structure which might be described as an archegonial jacket was observed. The cells bordering archegonia are large in some places and very small in others. When large, their nuclei are sometimes correspondingly large, which may lead to the impression that a few scattered jacket cells are present. There is no indication that a ventral nucleus is formed in any of the species. Miss Robertson (12) illustrated one instance in which the mitotic figure in the formation of a ventral nucleus is suggested, but from her account this appearance must be very rare. There is no megaspore membrane. If a megaspore membrane is present, it is so thin that it cannot be distinguished from the walls of the marginal cells of the female gametophyte.

Fertilization was observed in several instances. Conditions in one of these are shown in figure 2, where the smaller male nucleus is found in intimate contact with the egg nucleus, but the nuclear membrane separating them has not disappeared. A spherical mass of abandoned cytoplasm (x) which usually stains deeply is observable at the right above the fusion nucleus. One of the nuclei at the left may be the smaller male nucleus, the other the stalk nucleus or the tube nucleus. In this archegonium 2 of 3 or more neck cells are shown at the left. Sometimes deeply staining chromidial bodies are included in this abandoned cytoplasm. These may at times include the remains of entangled neck cells. In figure 3, where dislodged neck cells are not included in the section, the cytoplasm of the male cell is also evident near the neck, and a similar smaller male nucleus is situated immediately above it. The same deeply-staining cytoplasm of the male cell x is usually found and is shown in the proembryos of figures 4, 5, 8, 9, 10, 11, and 12. The smaller male nucleus and sometimes traces of the stalk nucleus are visible in some of the sections.

The separation of the male nuclei from the cytoplasm of the male cells could not be observed in *T. nucifera*. However, in one of the preparations of *T. taxifolia* the extrusion of male nuclei was observed. A highly magnified drawing of this section is shown in figure 14, which includes the lower end of a pollen tube touching an archegonium at the time of fertilization. The

male nuclei have at the time of their extrusion the form of an hour glass. The larger male nucleus has almost completed its emergence while the smaller male nucleus is just beginning to pass to the exterior. It will be noted that the two male cells do not become separated into distinct cells, so that a common mass of the male cytoplasm of both cells is left behind; in fact this might be spoken of as the cytoplasm of the body cell. These naked nuclei pass into the archegonium while the deeply stained abandoned cytoplasm remains behind. As shown in figure 14 this abandoned cytoplasm of the male cells may remain in the pollen tube. In *T. nucifera* figure 5 shows it above the neck, figures 2, 3, 8, 9, and 10 show it inside the upper region of the archegonium, but it is clear that in no case is the abandoned male cytoplasm included in the proembryo.

The manner of extrusion of a nucleus from the male cytoplasm in its hour-glass form resembles the condition found in *Sequoia sempervirens* (3), except that in the latter species the male cells first become separated from each other and take on a tear-drop form, with the nuclei emerging from the pointed end inserted into the necks of the archegonia.

About 28 proembryos of *T. nucifera* were observed in stages similar to figures 2–13. Figure 3 shows the 2-nucleate stage, figure 4 the 4-nucleate stage with walls beginning to form, and figure 5 the same stage with walls completed. The proembryo therefore occupies the lower half or two-thirds of the archegonium. This is in agreement with Miss Robertson's findings shown by her figures 23–26, plate 9, but appears to differ from *T. taxifolia*. This difference in the latter species is not so real as it seems, for in *T. taxifolia* the pollen tube not only destroys the neck cells, but invades and distorts the upper portion of the archegonium.

In *T. nucifera* the region occupied by the proembryo is limited to a zone of dense cytoplasm; within it is a denser zone close to the nucleus or nuclei. Actually this cytoplasmic zone is completely filled by the proembryo in all Torreyas. In *T. nucifera* and *T. californica* this denser zone of cytoplasm, and therefore the proembryo, occupies little more than half of the archegonium, while in *T. taxifolia* where the pollen tube has invaded the upper part of the archegonium this region of denser cytoplasm is the only part of the archegonium that is recognizable. Consequently, one usually finds the walls in the proembryo of the latter extending across this entire space, and this circumstance gives the impression that the proembryo fills the entire egg.

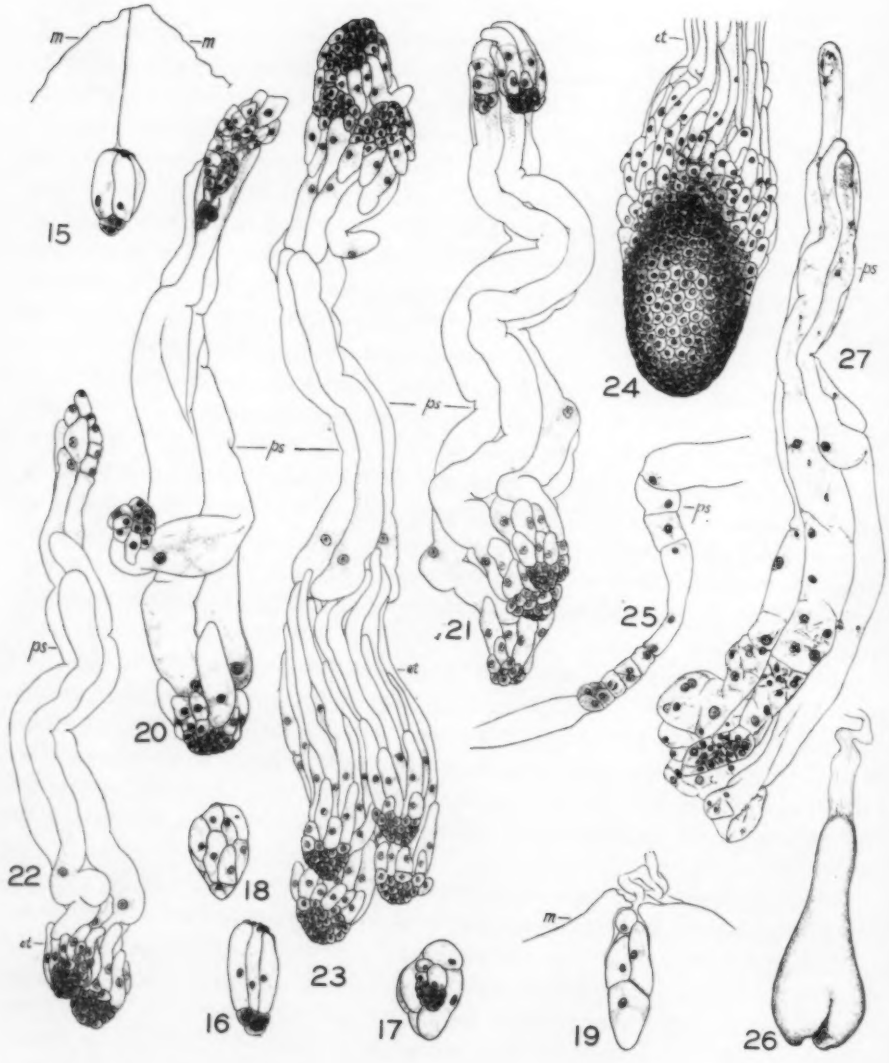
With this explanation for the apparent exception in *T. taxifolia,* the proembryo is in agreement with other Taxads and with conifers generally. It would not fill the entire archegonium if the entire archegonium were still present.

The divisions are not always regular in subsequent stages, and so give rise to the 6-celled, 8-celled and 12-celled proembryos shown in figures 7, 9,

and 10. Figures 8 and 11 seem to be embryos in a slightly later stage with 14–16 cells. In these stages the upper tier of cells or the entire proembryo elongates, soon fills the archegonium, and crowds the surrounding tissues. The proembryo becomes an arrested embryo through the late fall, winter, and early spring. I shall call this winter stage the *hibernal* embryo.

In late May or early June of the subsequent season the ovules enlarge rapidly. In ovules which had enlarged to sizes between 9 and 18 mm. long and between 6 and 10 mm. wide, the embryos were still found as hibernal embryos. Coulter and Land state that the proembryo of *T. taxifolia* remains dormant during the enlargement of the gametophyte as it develops into a ruminating endosperm. This same condition was found in *T. nucifera*. Figure 15 shows an hibernal embryo imbedded in the micropylar tip of the female gametophyte, whose upper boundary is shown by the line *m*. Figure 16 shows a similar hibernal embryo. Several others similar to these were found in a dozen gametophytes, which were successfully dissected from well-enlarged ovules. Here only two distinct tiers of cells are found if all of the shaded cells below are counted as belonging to the same tier, or there are three tiers if more than a single tier is counted in the group of cells below, whose number and arrangement is variable. These are all past the proembryo stage according to the more precise definition of the term proembryo, since some of the cells had begun to elongate before they were arrested in growth to form the hibernal stage. *Hibernal* is a term which carries the implication that they are slightly past the true proembryo stage, and remain relatively inactive throughout the late autumn, winter, and early spring. I am using the term *prosuspensor* for the group of 4 or more cells in the proembryo which elongate; these same suspensor cells are spoken of by previous investigators as suspensor or primary suspensor. Sometimes a canal or other faint line may be seen above the hibernal embryo leading upward to the nucellus. This passage marks the region above the archegonium which became closed as the gametophytic tissue grew up around the proembryo to imbed it.

The condition shown in the hibernal embryo of figure 17 was found several times. Figure 18 shows one of several hibernal embryos in which only one small cell near the lower end contained dense cytoplasm, and in which most of the prosuspensor cells in the tiers above were short, as if their elongation had included two tiers of cells, now slightly displaced. All of the hibernal embryos referred to above were deeply imbedded within the tip of the female gametophyte, but that shown in figure 19, situated much nearer to the surface, presents an unusual arrangement of cells in an hibernal stage which includes only five or six cells. Its elongated shape seems to indicate that it has suffered considerable distortion during its envelopment by the margin of the female gametophyte. It did not become as deeply imbedded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as usual and the remains of the pollen tube may be seen crushed against the top. Figure 19 is, no doubt, abnormal but it is reproduced because it indicates that the hibernal embryos may owe the variability in their internal cell-orientations and arrangements to accidental displacements suffered during the period when the gametophyte envelops the proembryo. Such arrangements as are found in figures 17 and 18 may be due, at least in part, to this cause. It seems probable that the embryo of figure 19 would, should it resume growth, push out and downward on the side facing the observer. Many of the irregularities observed in later stages may be attributed to variations in cell number and arrangement in the hibernal embryo.

In the proembryo stages of September and October collections, 3 of 28 ovules with proembryos were found in which two eggs had been fertilized. Figure 13 shows a pair of proembryos resulting from the fertilization of neighboring archegonia. To sum up, while usually only a single archegonium is fertilized, plural fertilizations were observed in about 10 per cent of the ovules. However, I have not recognized such pairs of hibernal embryos in about 18 ovules that were beginning to enlarge in the spring. These should be easily recognized by dissection.

The next stage obtained was from ovules which had grown to full size. These embryos are shown in figures 20–22. In each of these we find several multicellular embryos, already beginning to form massive secondary suspensors, attached to the lower end of the fully elongated prosuspensor composed of 4 or 5 cells. One of these, probably the largest terminal embryo, is destined to become the dominant embryo which survives in the matured seed, where almost invariably only a single embryo remains. Above the prosuspensor a group of cells is usually found which are in the position of rosette embryos. However, an examination of the series of arrested proembryos indicates that there is usually no rosette tier. They may have come from the subdivision of some of the cells of the hibernal embryo which did not elon-

Explanation of figures 15–27

FIGS. 15–26. *T. nucifera*. FIGS. 15–19. Hibernal embryos. × 55. FIGS. 15–16. As found imbedded near tip of female gametophyte near micropyle with margin of endosperm shown at *m*. FIG. 17. Proembryo with cell arrangement disturbed so that embryonic cells are beside prosuspensor cells. FIG. 18. Proembryo with larger number of cells. FIG. 19. Proembryo abnormal owing to disturbance caused by overgrowth of female gametophyte. FIGS. 20–22. Early embryo with prosuspensors elongated (from full grown ovule). × 45. FIG. 23. Slightly older embryo system after terminal embryos have developed massive secondary suspensors and several embryos have developed in region above prosuspensor. × 45. It is possible that these upper embryos belong in the same position as those in figure 21, and were disturbed in dissection and mounting. FIG. 24. Largest embryo obtained before cotyledons have appeared. × 55. FIG. 25. A single prosuspensor cell from an older embryo system which has given rise to embryonic masses. × 55. FIG. 26. Mature embryo dissected from seed. × 18. FIG. 27. Isolated prosuspensor of *T. californica* showing embryos developing from cells of prosuspensor, at first by free nuclear division followed by wall formation and ordinary cell division.

gate in the uppermost tiers of the prosuspensor, situated in such hibernal embryos as those shown in figures 17 and 18. In figure 21 a pair of small embryos is shown in the position of rosette cells. Figure 23 shows three embryos in this position apparently growing in the direction of the micropyle. However, one cannot be certain that these embryos were actually oriented in this inverted position within the gametophyte before dissection. It is entirely possible that embryos in the position above the prosuspensor shown in figure 21 may have become folded upward during dissection or subsequently during staining and mounting to give the appearance of figure 23. None of the embryos appears to have apical initial cells.

The prosuspensor cells in all of these figures (figs. 20–23) are uninucleate. In an older embryo system of which figure 24 represents the largest terminal embryo, some of the prosuspensor cells have several nuclei. Possibly some of these prosuspensor cells are beginning to form internal embryonic masses. Figure 25 shows an abnormally developed embryonic mass of cells found among the prosuspensor cells of another embryo system, which may have been derived from the subdivision of a prosuspensor cell. However, its diameter is much less than the usual size found in these cells. This is mentioned because of the peculiar behavior of the prosuspensor cells usually observed in *T. californica*, which is not shown, save for a few exceptions, in this species.

The embryogeny of *T. nucifera* includes no primary suspensor. Immediately below the prosuspensor a massive secondary suspensor is found, which is formed from the elongation of cells situated in the proximal region of the embryo. The terminal embryo shown in figure 24 has formed a massive secondary suspensor and is becoming cylindrical, but is still without internal organization of tissues. Soon after this stage the plerome of the root tip, the stem tip, and cotyledons would be expected to become organized. I obtained no embryos in this stage, but figure 26 shows (on a scale of magnification one-third that of figure 24) the mature embryo with its cotyledons, as it was removed from a ripe seed of *T. nucifera*. Its cotyledons are very short and have a retuse or slightly indented tip. The embryo occupies only a relatively small space, restricted to the axis of the upper fifth of the endosperm. When compared with the embryos of other conifers the embryo of this species is still relatively immature when the seed is ripe; it must still undergo considerable development within the seed after planting, before any part of it is ready to emerge from the seed coats. Several dozen were dissected from seeds and they were almost all of the same size and stage of development as in figure 26.

The endosperm or matured gametophytic tissue shows a distinct irregularity in its outer surface, due to the rumination of the female gametophyte. Rumination is less extensive than in other species. The sinuses shown in a cross section of the seed are not so deep or so numerous as those of *T. cali-*

fornica or *T. taxifolia*. There are usually three principal sinuses which extend less than half way inward from the margins to the centre and there are many minor corrugations.

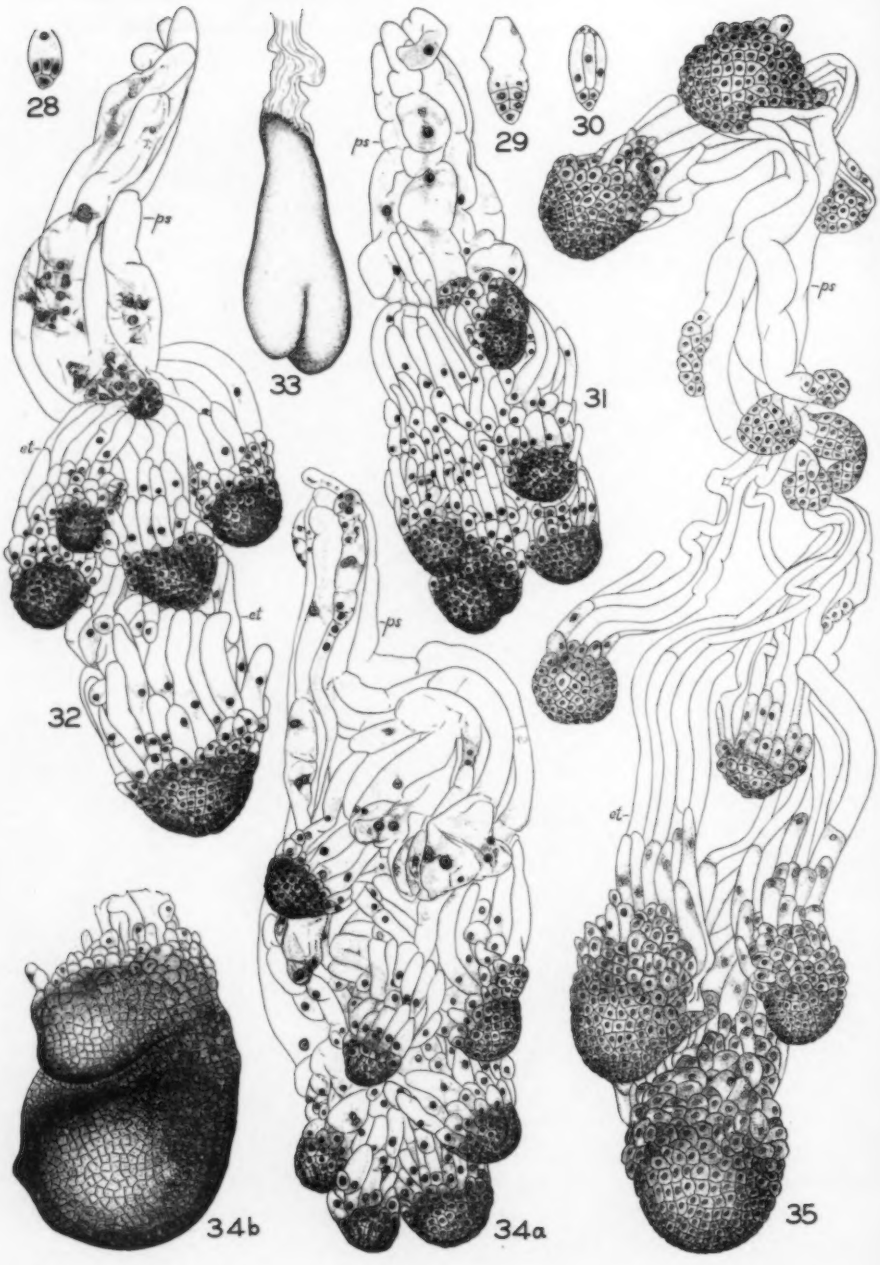
Torreya californica. In this species the hibernal embryos were not observed. Miss Robertson has shown the initial steps in the organization of the proembryo. Three of her proembryo stages are somewhat diagrammatically reproduced in figures 28–30, redrawn at the same scale of magnification as my figures of dissected embryos. They are from very early stages, soon after fertilization, and before the gametophyte has enveloped them. There is little doubt that these proembryos will still undergo enlargement before they become dormant or inactive, and should not be considered the equivalents of the hibernal embryos of figures 15–18, as found in *T. nucifera* in the subsequent season.

According to Miss Robertson's account of the proembryo, the two nuclei resulting from the first division of the zygotic nucleus are found in the lower part of the archegonium. Another nuclear division follows before any walls are formed. The upper nuclei, still incompletely walled off from the upper cytoplasm of the egg (figure 28), undergo additional divisions, which result in a proembryo with several tiers of cells. Figure 29 shows this stage, which has a terminal cell below, above this a tier of two or three cells, and four or five cells forming the prosuspensor tier. Above these are several relict nuclei which soon disintegrate. Following one or two other investigators of this period Miss Robertson labeled these upper nuclei the rosette, but the latter term should be applied to walled cells, above the prosuspensor, which fail to elongate. The prosuspensor tier elongates until it fills the archegonium completely, crushing the remains of the relict nuclei above them (figure 30).

While the proembryo of *T. californica* has not been observed in later stages or in the hibernal stage in the subsequent season, it may be presumed to enlarge considerably from the size shown in figure 30. The hibernal embryos shown for *T. nucifera* and those of *T. taxifolia* must for the present serve to supply this gap in the embryogeny of *T. californica*, with an allowance for size, since the archegonia of the latter are larger at the time of fertilization.

There is also the possibility that, at least occasionally, there may be two or more hibernal embryos in *T. californica*, resulting from the fertilization of eggs in separate archegonia. Of course, plural fertilizations would depend also upon the presence of more than one pollen tube, since the archegonia are separated so that only one egg may be fertilized by a pollen tube. For these reasons it is not certain that more than a single hibernal embryo would be found in *T. californica* except in well-pollinated material.

Figure 32 represents an embryo system of *T. californica*, in a stage comparable to the older stages shown for *T. nucifera*. There are four prosus-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pensor cells, bearing five embryos below on massive secondary suspensors, and a smaller embryo in which the secondary suspensor has not developed. As in *T. nucifera* there is no primary suspensor, and no apical initial cell. The nuclei in the elongated cells of the prosuspensor have divided a number of times, and cell walls are beginning to form as the ends of these prosuspensor cells are becoming embryonic.

Figure 27 shows a prosuspensor of *T. californica* which has been isolated from a system and which shows how its cells give rise to embryos after they have become elongated. The first steps are free nuclear divisions, followed by wall formation after a considerable number of separate nuclei have been formed; then cell plates begin to appear after each nuclear division. The embryos formed by this manner of budding from prosuspensor cells are often very misshapen and abnormal in appearance.

Figure 34*a* shows a similar embryo system which is considerably older. Six or seven prosuspensor cells and also a larger number of embryos are found. The largest embryo, on the end in this system, was broken off in dissection and is shown separately in figure 34*b*. It is two-lobed, a feature which may be only a later development of an embryo similar to the terminal one shown in figure 31. It was found difficult to dissect out the entire embryo system intact when the largest terminal embryo was of the size shown in figure 34*b*. These oldest embryos were firmly imbedded in the endosperm and could be obtained only by removing the gametophytic tissue around them a little at a time. Figure 35 shows the largest embryo system of *T. californica* which was successfully removed. Here the prosuspensor cells have all formed embryos from their lower ends by a process of budding, and well developed secondary suspensors have been formed in the larger embryos. There are a few embryos situated above the prosuspensor which may have developed from the upper end of some of the prosuspensor cells as shown in figure 34*a*, where one of the cells of its prosuspensor is in an early stage of budding above.

It is also possible that figure 35 may represent the embryos of more than one zygote, on the supposition that two archegonia were fertilized (by separate pollen tubes) and became closely associated as hibernal embryos. In this figure the prosuspensors do not show the upper origin clearly.

Figure 32 has four elongated cells in its prosuspensor, but in figure 34*a* there are at least six or seven. Miss Robertson places the number of such cells

Explanation of figures 28–35

FIGS. 28–35. *T. californica.* FIGS. 28–30. Proembryos in stages before dormancy. × 55. after Robertson (13). FIGS. 31–35. System of embryos dissected from fully enlarged ovule. Probably a larger terminal embryo is missing in figure 31 where prosuspensor cells *ps* are becoming multi-nucleate. × 55. FIGS. 32, 35. Complete embryo systems. Cells of prosuspensor *ps* becoming embryonic. × 55. FIG. 33. Embryo as dissected from fully matured seed. × 18. FIG. 34*a*. Embryo system, with its terminal embryo shown in FIG. 34*b*. × 55.

in the proembryo immediately after fertilization at five or six, but it is possible that their number may sometimes be increased or decreased by rearrangement of cells or by an abortion of cells in the hibernal embryo.

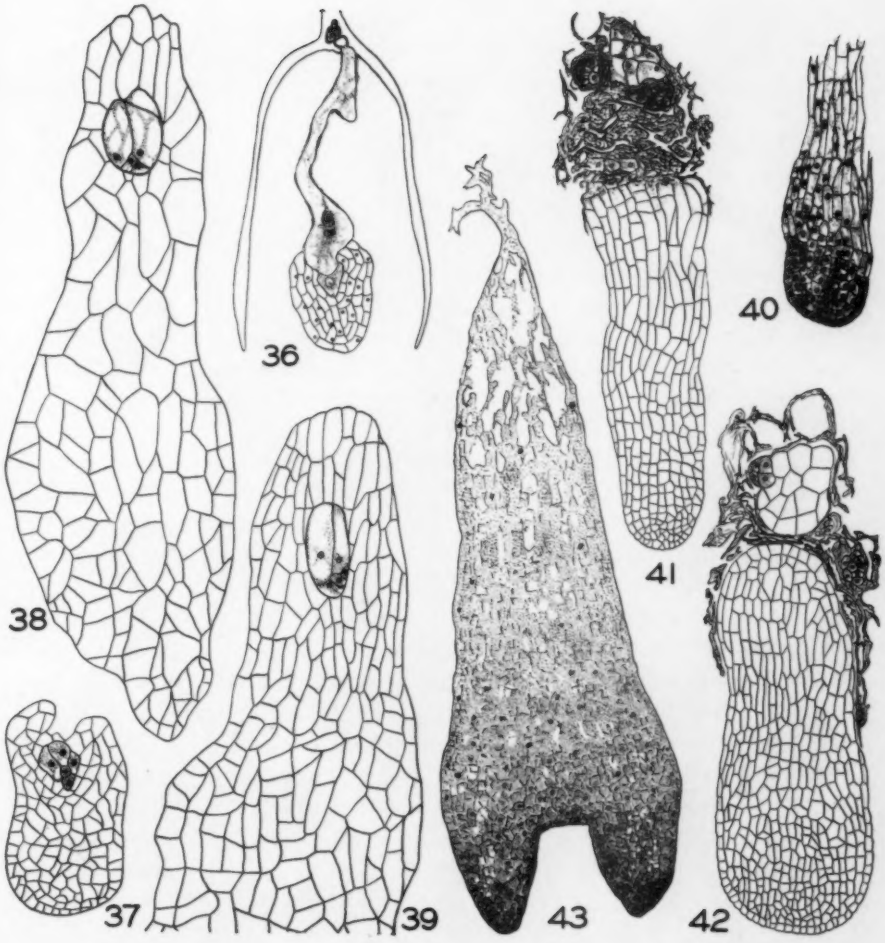
From living ovules no embryo was obtained larger than that showing in figure 34*b*. In this embryo primordia of the cotyledons had not been formed. Two cotyledons were found in the seeds of this species, and they are probably formed as in the other species, except that the embryo is larger in all comparable stages. Figure 33 shows an embryo dissected from a matured seed of the species at one-third the magnification used in the other illustrations. This embryo has a different form from that of *T. nucifera*, has longer cotyledons whose ends are rounded and are unequal in length. The entire embryo is somewhat larger. However, even this embryo is still very immature in a fully matured seed when compared to other genera of Taxads and to other conifers.

The general impression gained from the previous accounts, which were very largely confined to the proembryo, was that simple polyembryony prevails. The surprising feature in the embryogeny of the Torreyas is the nature and extent of their cleavage polyembryony. It appears that each zygote may produce at least as many embryos as there are cells in the early proembryo, sometimes as many as there are cells in the hibernal embryo. Even the prosuspensor cells of *T. californica* add more embryos to the large number which would have their origin from the cells of the lower tier or tiers of a proembryo.

The endosperm is more extremely ruminated in this species than in *T. nucifera*. The sinuses are more numerous and extend more than half way to the center of the endosperm.

Torreya taxifolia. Coulter and Land have given a detailed account of the development of the gametophytes, fertilization, and proembryo of *T. taxifolia*.

The mean dimensions of 7 female gametophytes of *T. taxifolia* before fertilization were found to be 173×270 μ. These dimensions are somewhat less than those given by Coulter and Land (200×300 μ). Their account must be modified only as explained in an earlier part of this description, since the cytoplasm of the male cells is abandoned and is not contributed to the zygote. The single archegonium of *T. taxifolia* would not be so much smaller than that of *T. californica* if it were still all present and fully recognizable at the time of fertilization. For the same reason the proembryo of *T. taxifolia* may fill the egg completely even before much elongation of the prosuspensor cells has taken place, and the latter may enlarge very little before the archegonium is completely filled. However, the prosuspensor cells do elongate and enlarge slightly during the period of enlargement of the female



FIGS. 36–43. *Torreya taxifolia*. FIG. 36. Relation of gametophytes in nucellus before fertilization. × 60. FIG. 37. Female gametophyte with proembryo being enveloped and passing into hibernal embryo. × 60. FIG. 38. Hibernal embryo in spring after beginning of enlargement of ovule. × 60. FIG. 39. Hibernal embryo in later stage showing upper half of endosperm. × 60. FIGS. 40–42. Sections of embryo on secondary suspensor with remains of smaller embryos resulting from cleavage polyembryony. FIG. 43. Section of mature embryo of seed. × 60.

gametophyte, as may be seen in the series of figures 36–39. This series of drawings serves to emphasize the small size of the gametophyte at the time of fertilization and shows the changes which take place in the gametophyte and embryo after fertilization. Figure 36 is a drawing reconstructed from four adjacent sections, showing the nucellus before fertilization, with the cavity occupied by the pollen tube after the latter has made contact with the archegonium. The pollen tube shows a body cell which is still undivided, and below it the stalk and tube nuclei. Figure 37 shows a stage of the gametophyte some time after fertilization, with a small proembryo completely filling the archegonium and becoming imbedded within the tip of the female gametophyte, which has enlarged slightly. Figure 38 shows a female gametophyte in the subsequent spring which has enlarged considerably, with the hibernal embryo completely imbedded. The female gametophyte shown in figure 39 has enlarged so much that only the upper half of it is shown. It has enlarged to a length of 2.5 mm. and is 5 or 6 times as long as that of figure 37. However, it is still to undergo a 10-fold enlargement in length before its full size is attained. Figures 37–39 show the relative inactivity of the hibernal embryo during this period of rapid growth of the female gametophyte, which may now be spoken of as endosperm. Coulter and Land state that the embryo during this period may consist of 12–18 cells. It is possible that some of the embryos (figures 37–39) do not have this number of cells, nor are they all organized in three tiers. However, the variations observed in the hibernal embryos of *T. nucifera* (figures 15–19) indicate that any differences in 2-tiered or 3-tiered organization may be of minor importance. As shown above, the corresponding stages in the hibernal embryos of *T. nucifera* and *T. taxifolia* pass through similar stages and, no doubt, those of *T. californica* do likewise, though they may be somewhat larger.

The stages which follow the elongation of the prosuspensor in *T. taxifolia* are probably very similar to figures 21 and 22 of *T. nucifera*. Figure 40 shows the cellular details of an embryo with the lower part of the secondary suspensor before the differentiation of the meristems that give rise to the root tip, cotyledons, etc. Figures 41 and 42 show later stages in which the remains of smaller embryos may be seen. They have been pushed upward by the rapidly elongating massive secondary suspensor.

Coulter and Land (5) mentioned the occurrence of secondary embryos observed in the second season, in the region above the secondary suspensor of the well enlarged embryo. No doubt they observed the conditions shown in figures 41 and 42. However, their suggestion that some of these may have had their origin in some kind of apogamy is superfluous in the light of the facts concerning the prevalence of cleavage polyembryony in the Torreyas.

Figure 43 shows a section of a mature embryo with its two cotyledons. This embryo is smaller than that of the other two species, since this figure

was drawn to the same scale as those of the younger embryos. These figures make it clear that cleavage polyembryony is also found in *T. taxifolia*, though it may be less extensive. Cleavage polyembryony is not as easily demonstrated from sections as from dissected preparations.

The endosperm is ruminated with deep sinuses and many other grooves and corrugations comparable to those of *T. californica*.

Austrotaxus spicata Compton. Figure 44 shows an embryo complex from the fertilization of 3 archegonia in *Austrotaxus*. This was dissected in 1927 from one of several ovules obtained from herbarium collections. This ovule had been preserved in formalin and came from one of Compton's original collections. The slide was left on deposit at the Arnold Arboretum. Unfortunately, the largest embryo was so firmly imbedded that it was broken off and not recovered, as shown by the broken ends of the prosuspensor.

By itself this single stage had little value. The writer had hoped to obtain additional material in earlier and later stages from which at least a partial account of the embryogeny might be given. In the meantime Saxton (15) has obtained sufficient material for a study of the morphology and proembryo. Figure 44 may, therefore, be included here because it adds a later stage to Saxton's account.

The striking feature shown by this figure is the very long prosuspensor. It also confirms the absence of cleavage polyembryony, as reported by Saxton, and the absence of a cap in the early embryo. The larger size and pointed shape of the archegonia shown by Saxton's figures, as well as the extent of elongation of the prosuspensor shown here, stand out in contrast with the small size of the archegonia and the relatively shorter prosuspensor found in *Taxus* (7, 8, 10). The only differences found between figure 44 and the oldest embryo illustrated by Saxton are the much longer prosuspensor and the absence of a rosette in each of the three embryos shown. Saxton found a rosette present at a much earlier stage of the embryo. It is not likely that I overlooked the remains of a rosette group which may have been present at an earlier stage, since I searched for these embryonic features with special care. The rosette is variable in its occurrence in some other conifers, notably in *Podocarpus spicatus*. A few scattered rosette cells have been observed in *Taxus* (8), but are found very rarely. The rosette is also variable in its occurrence in *Sciadopitys* and elsewhere. The difference between Saxton's record and my figure of the embryo is, therefore, not important except as it may indicate a similar variability in *Austrotaxus*.

At the time when the embryo of figure 44 was dissected out, I was especially interested in the possible occurrence of binucleate cells in the early embryo of conifers. Binucleate cells have been found in the early embryos of fourteen species of Podocarpaceae and only in the embryos of mem-

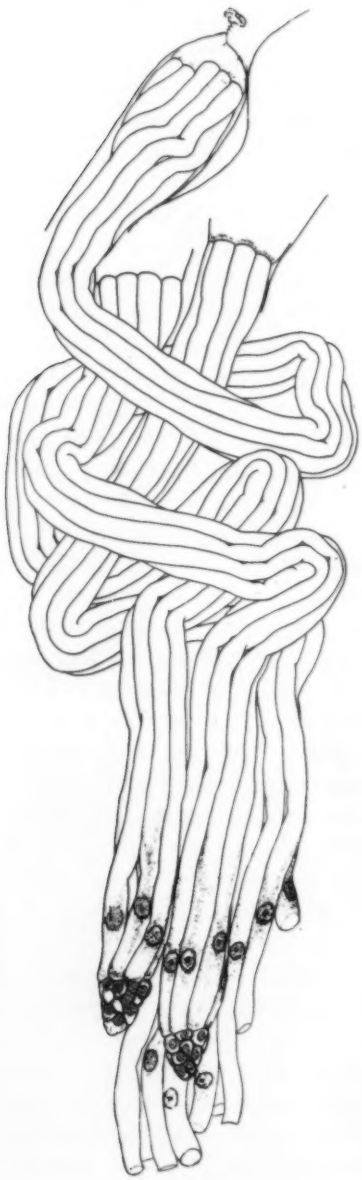


FIG. 44. Embryo system from an ovule of *Austrotaxus spicata*. From collection of Arnold Arboretum. ×90.

bers of this family. This includes *Saxegothaea conspicua*, investigated very recently by Doyle (6). While figure 44 does not show binucleate cells, I concluded at the time that these embryos may be past the stage when they would be binucleate. It is, therefore, significant that Saxton did not observe a binucleate condition in his earlier stages, nor has anyone found this condition in genera belonging to families outside of the true Podocarpaceae. Saxton's investigation has shown the absence of the terminal cap cell or group of cells at the end of the proembryo and early embryo; this is likewise indicated by my figure. The deciduous cap of the embryo was first observed by Strasburger in *Cephalotaxus Fortunei* (18), and has been confirmed by more recent investigators. The embryo of *Amentotaxus* has not been investigated; Saxton indicates that it bears a close resemblance to *Cephalotaxus*.

Saxton, who reviewed the comparative morphology of this group, concluded that *Austrotaxus* is a form which stands in a position intermediate between *Taxus* and a prototype which may be common to *Cephalotaxus* and *Amentotaxus*, as well as to the Torreyas. All of the new embryological facts brought out by my investigation are in general agreement with Saxton's scheme of phylogeny.

DISCUSSION

Fertilization. The process of fertilization undoubtedly merits additional investigation in conifers. The record has stood for many years that cytoplasm of the male cell contributes to the fertilized egg in *Torreya*, but I have found the evidence to the contrary. Land (9) made the statement in his study of *Thuja occidentalis* that only the nucleus enters into the zygote, and several of his figures show the abandoned cytoplasm at the neck of the archegonium. However, a few years later Coulter and Land (5) described fertilization in *Torreya taxifolia* as including male cytoplasm. Miss Robertson (13) had pointed out and Coulter and Land also showed a sheath of denser cytoplasm surrounding the fusion nucleus. The presence of this cytoplasmic sheath in *Torreya* seems to be the only evidence offered for the inclusion of male cytoplasm.

That this distinct cytoplasmic sheath may have a different origin is indicated by the fact that it is already beginning to appear before the egg is fertilized (see figure 14). It is shown in Coulter and Land's figure 23, plate II, also, less distinctly, in Miss Robertson's figure 14, plate 8, both of unfertilized eggs. Even if this zone becomes more pronounced after fertilization it is unnecessary to assume that it had its origin in a contribution of male cytoplasm.

None of the previous investigators of *Torreya* mentioned the abandoned cytoplasm of the male cells which is left behind. However, it is shown at the right of the neck of the archegonium in Coulter and Land's figure 24, which shows that a naked male nucleus below is crossing the dense zone of cytoplasm

in fertilization. Miss Robertson (13) shows the abandoned mass of male cytoplasm in figures 19, 23, and 24 of plates 8 and 9, where it is the largest of the objects labeled *n.c.* This abandoned cytoplasm is devoid of a nucleus but sometimes contains chromidial bodies.

Sinnott (17) shows a very distinct zone of deeply-staining cytoplasm surrounding the egg nucleus before fertilization, as well as after fusion of the sexual nuclei, in *Podocarpus ferrugineus* and *Dacrydium Bidwillii* in his plate V, figures 2 and 3. His photomicrographs, figures 34 and 41, show this for *P. dacrydioides*, before fertilization. In his figure 35 the sheath of dense cytoplasm is present on all sides of the egg nucleus before the male nucleus has made contact. Furthermore in figures 36 and 42, showing the first division of the sporophyte, this zone is less distinct than before fertilization; in figure 42 this zone is destroyed on the upper side where the male nucleus passed through it, where it would be expected to be most abundant if actually contributed by the male cell.

I feel convinced from my own investigations of *Torreya* that the dense zone of cytoplasm surrounding the fusion nucleus before and after fertilization is not the male cytoplasm, and that the male nucleus which fuses with the egg nucleus is shed from the cytoplasm of the body sells. Only a negligible trace of male cytoplasm from any source is likely to enter into that region of the egg which is likely to be included in the embryonic cells of the proembryo.

A new feature which was observed indicates that in Torreyas the male cells do not become separated from each other. The two male nuclei emerge at different places in the common cytoplasm of the double male cell.

Phylogeny. There is little doubt about the fact that *Torreya* is a highly specialized genus of the Coniferae. All species of *Torreya* have wingless pollen grains without prothallial cells, have unequal male nuclei in their pollen tubes, and none of the features associated with the more primitive conifers. The absence of a megaspore membrane, the fact that walls appear in the proembryo after 4 free nuclei have formed, the small archegonia with absence of an archegonial jacket, the specialized condition of an hibernal stage in the embryo associated with the prolongation of the embryogeny into two seasons, dicotyledonous embryos, and the ruminating endosperm are all advanced features. The ovule is at maturity the largest and most specialized of those of all the conifers.

Torreya nucifera shares with *T. californica* all the primitive features of the gametophytes and embryo. Like the other vegetative and reproductive structures, the female gametophytes may be larger in the latter species; the archegonia also are considerably larger, differing in about the same ratio or possibly more. Otherwise, however, in the number of archegonia, in the

number of their neck cells, in the general character of the proembryo, which occupies only the lower portion of the egg, these two species are in very close agreement. It is also possible that the occasional plurality of hibernal embryos resulting from the fertilization of two archegonia in *T. nucifera* may be duplicated in *T. californica*, in well pollinated material. This feature cannot be duplicated in *T. taxifolia*, in which there is usually only a single archegonium.

The three species agree further in having walls appear in the proembryo after the four nuclei have been formed, a condition which seems to be unaffected by variations in the size and shape of the archegonia. The three species have similar conditions of cleavage polyembryony, with a number of embryos resulting from various cells in the hibernal embryo. However, *T. californica* adds to the polyembryony through budding, resulting from extensive subdivision of the tips of the prosuspensor cells. It appears that all three species may have embryos in the position of rosette embryos, and there is no essential difference, save that of size, in the matured embryos of the seeds. They are all dicotyledonous, with the possibility of inequality of length in cotyledons of *T. californica*.

With respect to the rumination of the endosperm both *T. californica* and *T. taxifolia* are much more advanced than *T. nucifera*. I have examined a considerable number of the latter but only a few of *T. californica*. Coulter and Land (5) have given an excellent photographic reproduction showing the shape and the extent of the rumination of *T. taxifolia*. *T. nucifera* shows the least complexity; the endosperm is described by Pilger (11) as folded or pleated and corrugated. The seeds which I examined had the three deepest longitudinal sinuses extending to less than half the distance to the center, and there were many smaller wrinkles and corrugations between them. *T. Fargesii*, which was not available for study, is described by Pilger as having its endosperm ruminated half way to the middle. The endosperm of *T. californica* and *T. taxifolia* has sinuses extending more than half way to the middle of the ovule. This agrees in general with the order given in Pilger's monograph, which treats *T. nucifera* first as the more primitive species, but it appears from the present study that *T. taxifolia* is the most specialized.

The advanced morphological features in the Torreyas are all found in *T. taxifolia*. In this species the pollen tube arrives relatively sooner and remains so long in contact with the archegonium that it not only destroys the pair of neck cells, but also shortens the archegonium, to give the appearance later of a proembryo which fills the entire archegonial cavity at the time of wall formation. These features, as well as the extreme reduction in the number of archegonia to one (very rarely two) marks this species as the most advanced. In general, therefore, the three species stand in the following phylogenetic order: *T. nucifera*, *T. californica*, *T. taxifolia*.

Saxton (16) in his study of the morphology of *Austrotaxus spicata*, points out the probable phylogeny of the Taxaceae, consisting of 5 genera which include *Torreya*. He considers three groups or branches derived from the same prototype and places *Torreya* by itself at the end of one branch, *Cephalotaxus* above *Amentotaxus* at the end of another, and *Taxus* at the end of another branch, with *Austrotaxus* as a more primitive form or connecting link.

It is only in following such an arrangement that the writer can relate to each other the groups included in the taxad genera. They have diverse embryogenies when compared. In *Taxus* and *Austrotaxus* simple polyembryony prevails, in *Cephalotaxus* we find simple polyembryony for the main terminal embryo, which is borne on the end of a prosuspensor and is terminated by a deciduous cap, but we have a form of cleavage polyembryony (determinate in character) since the rosette cells give rise to small embryos. None of the groups has the deciduous cap in the early embryo except *Cephalotaxus*. Thus, one group represented by *Torreya* has retained cleavage polyembryony while both of the other two groups have lost it. One of them shows distinct evidence of having been derived from a prototype with cleavage polyembryony, while the other shows the evidence for such a history less distinctly, but the embryonic cells still possess the potentialities.

In support of the latter statement we need only to refer to Jäger's (8) observations on *Taxus*, which the writer has verified in part. Jäger states that the suspensor cells which do not elongate fully but become separated from the rest (of the prosuspensor) undergo nuclear divisions, and form embryos within these cells. He illustrates several misshapen embryos of this kind in plate XIX, figures 75*a*, 75*b*, 75*c* and 75*d*. As he states, not only the terminal group of cells which actually contribute the embryo are embryonic, but also the cells of the upper tier strive to form embryos, which become aborted soon after they form a tissue of several cells. This also marks the group of elongating cells in *Taxus* as constituting a prosuspensor, and these potentialities support the view that cleavage polyembryony may have been present in the history of *Taxus*, although it is the genus in which it is now most completely eliminated. Of course, Saxton's phylogenetic arrangement, which I am accepting, is supported by many other morphological facts.

SUMMARY

1. *Torreya nucifera* is similar to *T. californica* in having from two to four (usually three) archegonia. *T. taxifolia* usually has only one archegonium.

2. None of the species of *Torreya* forms the ventral canal nucleus.

3. The megaspore membrane is absent in all species, or so thin that it is not usually observed.

4. The female gametophyte is smallest in *T. taxifolia*, somewhat intermediate in size in *T. nucifera*, and is largest in *T. californica*, at the time of fertilization.

5. The pollen tube in *T. taxifolia* reaches the female gametophyte very early, sometimes before cell walls are formed, and is in intimate contact with the archegonium throughout its development, invading and digesting the neck cells and the upper portion of the archegonium. In *T. nucifera* the neck cells persist and vary in number from two to eight. The usual number is four.

6. At fertilization the male nuclei are released from the cytoplasm surrounding them in the double male cells, which do not become separated. This abandoned cytoplasm is usually found in the upper portion of the egg, where it does not contribute to the cytoplasm included in the zygote.

7. The proembryo of all three species of *Torreya* forms four free nuclei before walls appear and, with the exception of that of *T. taxifolia*, the proembryo occupies only a portion (about two-thirds) of the space in the archegonium; in the latter species, where a part of the archegonium is destroyed, it may occupy all of the space that remains.

8. The proembryo passes into an 8-celled stage; from this into a proembryo of 12–16 cells, in which the tiers are not equal in the number of their cells and the cells not always arranged in distinct tiers. This is followed by a slight elongation of the prosuspensor cells in the uppermost tier, followed by an inactive period to form the hibernal embryo.

9. In *T. nucifera* more than one archegonium may sometimes be fertilized, giving rise to two embryo systems. In *T. taxifolia*, which has only a single archegonium, only one embryo system is possible.

10. Cleavage polyembryony is a constant feature in *Torreya*. In the season following fertilization the hibernal embryo forms a system of several embryos borne on the end of a prosuspensor of from three to five or more elongated cells.

11. Embryos may arise in the rosette region, but the exact manner of origin of rosette embryos remains uncertain and may be variable.

12. In *T. californica* the prosuspensor cells may become multicellular by division of their nuclei and give rise to additional embryos through a form of budding in the second season. In *T. nucifera* budding from the prosuspensor cells was not usually found.

13. The mature embryo of the seed has two cotyledons in all three species. In *T. californica* the cotyledons were found to be unequal in length.

14. The female gametophyte forms the endosperm, which is only slightly ruminated in *T. nucifera*, and becomes very deeply ruminated in *T. californica* and *T. taxifolia*.

15. *Torreya* occupies a very high position in the phylogeny of conifers.

The species of *Torreya* may be arranged in the following order of complexity: *T. nucifera*, *T. californica*, and *T. taxifolia*.

16. The phylogeny of Taxaceae suggested by Saxton has been confirmed.

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MACROSPOROGENESIS AND THE DEVELOPMENT OF THE EMBRYO SAC IN YUCCA ALOIFOLIA

FRED T. WOLF

(WITH FIFTEEN FIGURES)

The development of the macrogametophyte or embryo sac in the Angiosperms has now been worked out in a considerable number of genera and species. Although no fewer than ten types of embryo sac development, involving variations in the number of functional macrospore nuclei and the number of nuclei in the mature embryo sac, are described in a recent review of this subject by Maheshwari (1937), perhaps 95 per cent of all the forms which have been studied are characterized by a "normal" development, involving the formation of an 8-nucleate embryo sac from a single functional macrospore.

The formation of the macrospores and the subsequent development of the macrogametophyte in the genus *Yucca* (Liliaceae, tribe Dracaenoideae or Yucceae) have been studied by a number of investigators. The hypodermal position of the archesporial cell and its division to form an outer parietal cell and an inner macrospore mother cell were observed by Vesque (1879), Guignard (1882), and Hérail (1889). Working with the same species, *Y. gloriosa*, all three of these investigators were led to believe that the division of the macrospore mother cell resulted in the formation of only three macrospores. The presence of an axial row of four macrospores in this genus was apparently first noted by Koernicke (1901) in *Y. filamentosa*, and has been confirmed by subsequent investigators.

Fairly complete accounts of the development of the embryo sac have been given for *Y. gloriosa* by Guignard (1882), for *Y. filamentosa* by Reed (1903), for *Y. glauca* by Folsom (1916), and for *Y. rupicola* by Watkins (1937). All species of the genus hitherto investigated have been shown to have an embryo sac of the "normal" type, the accounts of the various investigators differing only in the arrangement of the macrospores in the tetrad and the identity of the functional macrospore.

The chromosomes of *Y. aloifolia* root tips have been studied by Müller (1910), who found that the diploid complement included 54–56 small chromosomes plus 10 large ones. More recently McKelvey and Sax (1933), in a number of species of the genus, report $n = 30$, consisting of 5 large and 25 small chromosomes.

MATERIALS AND METHODS

The species which forms the basis of the present report is *Yucca aloifolia* L., which is described and illustrated in the monograph of Trelease (1902).

Flower buds of various sizes were collected in July 1938 from plants growing near the Duke University Marine Laboratory, on Piver's Island, near Beaufort, North Carolina. Securing the desired variety of developmental stages was greatly facilitated by the fact that the inflorescences contain flowers of different ages, a given stalk bearing very young buds at the apex and at the same time mature flowers ready for pollination near its base. The pistils were removed from the buds, the larger ones being sliced into several pieces to insure thorough penetration of the fixative, and fixation was carried out using Karpechenko's modification of Navashin's solution. After washing, the material was dehydrated and cleared in an ethyl alcohol-butyl alcohol series, and imbedded in paraffin. Transverse sections of the pistil were cut at a thickness of 10 μ, and the sections were stained with Heidenhain's iron alum hematoxylin.

OBSERVATIONS

The ovary in *Y. aloifolia*, like that in other members of the genus, is superior, and consists of three fused carpels. Placentation is axile, and cross sections of the ovary show that the anatropous ovules are borne in six rows, two in each locule.

The youngest ovules examined show, near the micropylar end of the nucellus, a macrospore mother cell and an outer parietal cell (fig. 1), resulting from the prior division of an archesporial cell which is hypodermal in position. The large nucleus of the macrospore mother cell contains a single nucleolus and conspicuous chromatic strands during the prophases of the heterotypic division. Chromosomes are differentiated and become aggregated on the equatorial plate (fig. 2). Following the completion of the heterotypic division, a cell wall is formed, separating the two component cells of the dyad (fig. 3). A metaphase stage of the succeeding homoeotypic division is shown in figure 4.

The meiotic divisions result in the formation of a tetrad of macrospores (fig. 5), which usually, although not always, show a "T-shaped" arrangement with the micropylar pair lying side by side. An axial row of four macrospores in a linear arrangement has been observed, but apparently this is of much less common occurrence, the "T-arrangement" being the rule.

Explanation of figures 1–7

FIG. 1. Macrospore mother cell and parietal cell. × 480.

FIG. 2. Equatorial plate stage of heterotypic division. × 480.

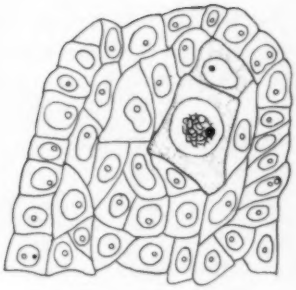
FIG. 3. Two cells resulting from heterotypic division. × 360.

FIG. 4. Equatorial plate stage of homoeotypic division. × 360.

FIG. 5. Tetrad of macrospores in "T-arrangement." × 360.

FIG. 6. Developing chalazal macrospore, with remnants of two disintegrating macrospores; two tapetal cells. × 480.

FIG. 7. Developing chalazal macrospore, with remnants of two disintegrating macrospores. × 480.



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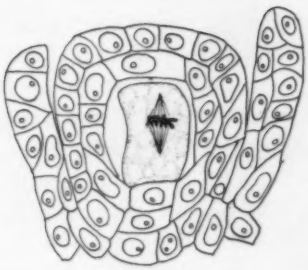

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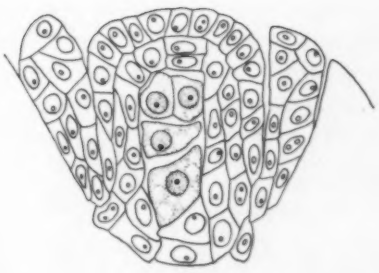

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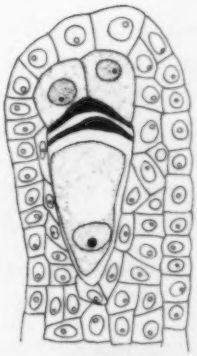

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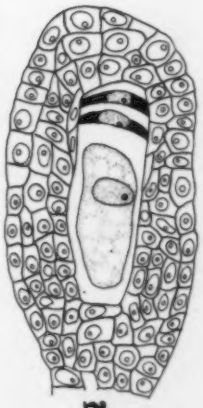

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The parietal cell, differentiated by division of the archesporial cell, divides during macrosporogenesis to form two tapetal cells (fig. 6), whose contents are soon to be utilized in the development of the macrogametophyte. In all cases observed with certainty, it is the chalazal macrospore which develops into the embryo sac.

As the chalazal macrospore enlarges, the three remaining macrospores are crushed, and their deeply-staining remnants persist for a short time (figs. 7–9). The nucleus of the functional (chalazal) macrospore then divides, the orientation of the spindle being in the direction of the long axis of the embryo sac (fig. 8), and a 2-nucleate macrogametophyte is formed (fig. 9). The second nuclear division, resulting in the formation of a 4-nucleate embryo sac, then occurs (figs. 10, 11), the orientation of the spindles in this case being transverse to the long axis of the embryo sac.

Meanwhile, the micropylar portion of the embryo sac has expanded laterally to a greater extent than the chalazal end, so that the embryo sac is more or less swollen toward the micropyle and tapers gradually toward the tubular chalazal end. The four nuclei divide again simultaneously (figs. 12, 13) to give rise to an 8-nucleate embryo sac. Three nuclei in the micropylar portion of the now greatly enlarged embryo sac become delimited by cell walls to form the egg apparatus, consisting of an egg cell and two synergids. Similarly, three of the chalazal nuclei become surrounded by cell walls to form the three antipodal cells in the narrow tubular portion of the embryo sac. The two remaining polar nuclei subsequently fuse to form the large primary endosperm nucleus of the mature 7-celled embryo sac (figs. 14, 15).

DISCUSSION

In macrosporogenesis and the development of the embryo sac, *Y. aloifolia* conforms in general to the "normal type" characteristic of the vast majority of angiosperms which have been investigated. The female gametophyte of *Y. aloifolia* is very similar to that of *Y. gloriosa* (Vesque 1879; Guignard 1882; Hérail 1889), *Y. filamentosa* (Reed 1903), *Y. glauca* (Folsom 1916), and *Y. rupicola* (Watkins 1937). Development of the embryo sacs of various species of *Yucca* seems to vary somewhat, however, in the

Explanation of figures 8–15

FIG. 8. Metaphase stage of first division in the embryo sac. × 480.

FIG. 9. 2-nucleate embryo sac. × 480.

FIG. 10. Telophase stage of second division in the embryo sac. × 360.

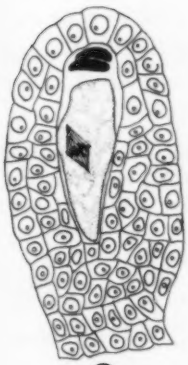
FIG. 11. 4-nucleate embryo sac. × 360.

FIG. 12. Prophase of third division in the embryo sac. × 360.

FIG. 13. Metaphase of third division in the embryo sac. × 360.

FIG. 14. 8-nucleate embryo sac, showing egg cell, two synergids, three antipodals, and the two polar nuclei. × 270.

FIG. 15. Mature 7-nucleate embryo sac; the two polar nuclei have fused to form the primary endosperm nucleus. × 270.



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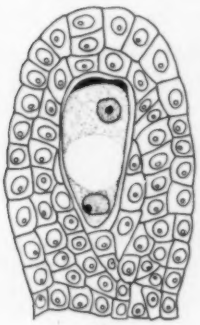

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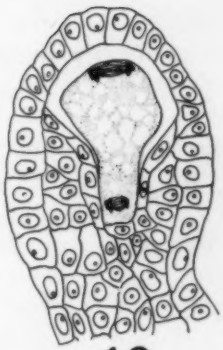

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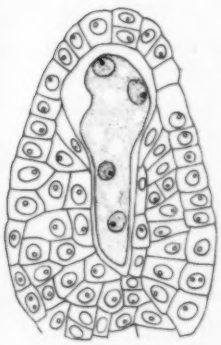

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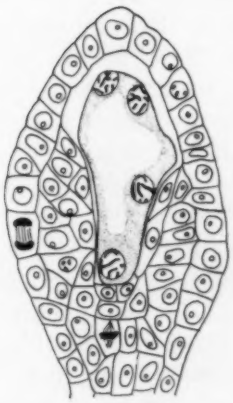

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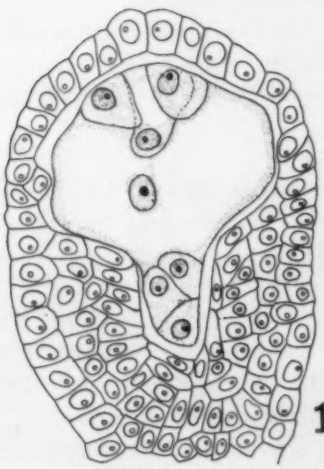

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arrangement of the macrospores in the tetrad. It would appear that the failure of early investigators to note the formation of four macrospores may be due to the fact that the micropylar pair often lie side by side, the tetrad thus having a "T-arrangement." An axial row of four linearly arranged macrospores occurs regularly in *Y. filamentosa* according to Koernicke (1901) and Reed (1903), and in *Y. rupicola* according to Watkins (1937). In *Y. glauca*, Folsom (1916) reports that the "T-arrangement" is usual, but an axial row also occurs frequently. In *Y. aloifolia* also the "T-arrangement" appears to predominate.

Another point of variance among the various investigators has to do with the identity of the macrospore which becomes functional in the formation of the embryo sac. According to Folsom (1916), in *Y. glauca* any one of the tetrad of macrospores may develop. Guignard (1882) reported that either the chalazal macrospore or the one lying immediately above it could form the female gametophyte. In *Y. filamentosa*, Reed (1903) states that in every case in which he was certain, the macrospore next to the chalazal one proceeded to develop into the female gametophyte. Formation of the embryo sac in *Y. aloifolia* is in accord with the findings of Hérail (1889) and Watkins (1937) in other species; in every case observed, it is the chalazal macrospore which develops.

The chalazal tube of the mature female gametophytes of *Y. filamentosa* and *Y. rupicola* has been considered by Reed (1903) and Watkins (1937) as being haustorial in function. It would appear that *Y. aloifolia* is essentially similar in this respect. Raciborski (1893), apparently the only previous investigator to study the embryo sac in *Y. aloifolia*, found that as a result of staining with a fuchsin-iodine green combination the nuclei of the egg apparatus and the polar nuclei stain red, while the antipodal nuclei are blue-staining. An explanation of this difference in staining reaction probably has to do with a difference in function. Perhaps the suggested haustorial function of the chalazal portion of the embryo sac, including the antipodals, may explain Raciborski's observations.

SUMMARY

In *Yucca aloifolia* L. macrosporogenesis results in the formation of a tetrad of macrospores, generally with a "T-arrangement," the micropylar pair lying side by side. The chalazal macrospore is the one which becomes functional in the formation of the embryo sac. The development of the female gametophyte is of the "normal type," the embryo sac at maturity being 7-celled. The chalazal portion of the mature embryo sac is tubular, perhaps serving an haustorial function.

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LIGHT AND THE GROWTH OF EXCISED ROOTS OF DATURA

WILLIAM J. ROBBINS

(WITH ONE FIGURE)

In experiments on the growth of excised *Datura* roots performed in part with the assistance of Mary Bartley Schmidt in 1938, observations were made on the effect of light on their growth. Although the number of roots observed was small and they were grown in a limited number of solutions the results were quite definite and may be of interest to others working in this field.

The excised roots were obtained from seeds supplied by A. F. Blakeslee and came from an inbred line of diploid *Datura stramonium*, lot no. 3702564. Seeds were sterilized with calcium hypochlorite and germinated on sterile water agar.

On August 18, 1938, a 5 mm. terminal piece of a seedling root was transferred to 50 ml. of modified Pfeffer's solution containing 2 per cent Merck's maltose and 100 p.p.m. Harris yeast. The root was placed in diffuse light at 23°–24° C. On September 5, after 18 days growth, it had reached a length estimated to be about 12 cm., but had formed no branch roots.

It was noted at that time that tufts of root hairs occurred along the length of the root at more or less regular intervals. The root was somewhat thickened at the places of heavy root hair production. The appearance of the root at this time is shown diagrammatically in figure 1. Thirteen groups of

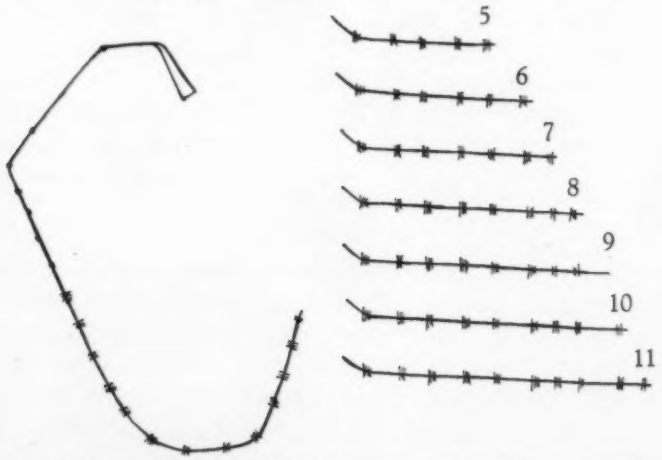

FIG. 1. Left, Excised *Datura* root after 18 days growth in diffuse daylight. Note tufts of root hairs at intervals. Right, Terminal portion of *Datura* root on September 5, 6, 7, 8, 9, 10 and 11. Kept in continuous darkness September 9. Note cluster of root hairs for each day except September 9.

root hairs from 3 to 6 mm. apart could be clearly seen and above these, nearer the base, were several swellings, some of which were the beginnings of branch roots.

Observations of the root were made daily, and it was found that a cluster of root hairs was produced each 24 hours during the daylight hours. Elongation occurred mainly at night, with short and scattered root hairs. During the daylight hours the root elongated slowly, thickened somewhat, and the root hairs found were long and close together. The development of the root on several successive days is shown in figure 1.

The relation of light to this phenomenon was confirmed by placing the root in a dark cabinet on September 8th. During the next 24 hours the root elongated, but no tuft of root hairs was found. The root was returned to the light on September 10th, and clusters of root hairs were formed on the 10th and 11th. Observations were discontinued at that time.

A second seedling excised root was grown in diffuse light in the maltose-yeast solution, and root hairs in tufts were noted, but no observations to relate the tufts to light and darkness were made. Subcultures of this root were grown in solutions containing thiamin and vitamin B_6, and as they developed in diffuse light the characteristic clustered root hairs appeared on parts of the root. Other portions developed thickenings at regular intervals, but few or no root hairs. The thickenings gave the root a beaded appearance and were assumed to be associated with alternate exposure to light and darkness.

It appeared, therefore, that growth in length of excised *Datura* roots under the conditions described was inhibited by exposure to light. With the inhibition of elongation a thickening of the root occurred, and frequently, though not always, long root hairs were produced freely on the thickened portion.

Unfortunately no microscopic studies were made which might have made clearer what occurred during the light period. It may be suggested, however, that when normal elongation was inhibited by light the internal pressure of the cells was not relieved by elongation and exerted its effect by increasing the crosswise diameter and pushing out the long root hairs. A similar explanation was offered for the failure of root hairs to develop on excised strips of the periblem and dermatogen of corn roots as contrasted to their development when the same tissues remained attached to the plerome (2).

A light effect of this character has not been reported for excised roots of other plants. Excised tomato roots seem unaffected by exposure to light (3, 4), and corn roots were stated by Robbins and Maneval (1) to be favorably influenced by light in some instances.

To speculate on how light produces its effect on the excised *Datura* root

is perhaps premature. Two obvious possibilities may be suggested. Light may produce inhibitors which are destroyed in darkness. This is not an unreasonable suggestion in view of the known facts of photosensitivity. On the other hand light may destroy growth substances formed in darkness and necessary for the elongation of cells. Auxins are destroyed by light and are concerned in cell elongation, but their relation to the elongation of roots is still somewhat obscure. If the second suggestion is correct, it would seem that the quantity of the growth substance in these roots is less than in tomato roots, for example, which do not appear to be sensitive to light; or that the conditions under which it exists in the *Datura* cells make it more sensitive to light than in tomato roots. Other possibilities could be suggested but their presentation will be delayed until more knowledge of the phenomenon is at hand.

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SOME NUCLEAR PHENOMENA IN VENTURIA INAEQUALIS[1]

E. J. Backus and G. W. Keitt

(with twenty-two figures)

The development of the ascocarp of *Venturia inaequalis* (Cke.) Wint. has been studied by Killian (1917) and Frey (1924), both of whom reviewed extensive literature dealing with sexuality in the Ascomycetes. Their work has been reviewed by Keitt and Palmiter (1938) in connection with studies on heterothallism and variability in this fungus. Observations on the cytology of the imperfect stage of this organism have been reported by Wiltshire (1915) and Nusbaum and Keitt (1938) in studies on host-parasite relations. Recent work by Keitt, Palmiter, and Langford (1938) and Keitt and Langford (1940) on variability and inheritance of this pathogen make desirable further investigation of the development of the ascus and of nuclear phenomena in the vegetative mycelium, the conidiophore, and the conidium. Such studies are reported in the present paper.

MATERIALS AND METHODS

Overwintered leaves collected in March and April of 1938 and 1939 from apple orchards at Gays Mills, Wisconsin, and Sturgeon Bay, Wisconsin, constituted the source of material for this investigation. The leaves were placed outdoors on sod under wire cages for development of the asci (*cf.* Wilson, 1928). From time to time leaves were brought into the laboratory and placed in a moist chamber for a short period. Prior to fixation, microscopic examination was made to determine the stage of development of the asci.

Formal-acetic alcohol was most extensively used as a fixative and proved most successful, although Allen's modification of Bouin's mixture also gave a number of favorable fixations. Carnoy's A, Carnoy's B, Conant's, and Navashin's solutions were tried, but all gave unsatisfactory results. Paraffin infiltration was accomplished by the butyl alcohol technique. Slides were prepared from the embedded portions of leaf by cutting microtome sections 7–8 μ thick and staining with Heidenhain's iron-alum haematoxylin.

In addition to the cytological preparations made in the above manner, supplementary slides of another sort were prepared by teasing out fresh ascocarpic material and crushing it in cotton-blue and mounting fluid.

EXPERIMENTAL RESULTS

The Ascus. By the use of both stained paraffin sections and crushed fresh ascocarpic material, it was shown in confirmation of the work of Killian

[1] This work was supported in part by grants from the Joseph Henry Fund of the National Academy of Sciences and the Wisconsin Alumni Research Foundation. Grateful acknowledgments are made to Professors M. P. Backus and E. M. Gilbert for advice during its progress.

(1917) that the asci of *Venturia inaequalis* are initiated by crozier formation. The crozier is formed when the tip of an ascogenous hypha bends and walls are formed in such manner as to make a uninucleate terminal cell and a binucleate penultimate cell. The nuclei of this cell fuse almost as soon as it is formed. Such a crozier with its fusion nucleus is shown in figure 1. This sub-terminal cell grows and develops into the young ascus. The primary ascus nucleus is large in proportion to the size of the cell, having a diameter equal to more than three-fourths that of the ascus at this stage. A large nucleolus and considerable amounts of darkly-staining chromatic material are observed. Very conspicuous beads of chromatin are present on the thin threads which wind throughout the nuclear cavity (fig. 2).

The ascus soon elongates and the nucleus divides. Figures 3–6 show examples of the first division. The spindle is intranuclear, at least a portion of the old nuclear membrane usually being visible. There appears characteristically to be a darkly-staining granule at each end of the spindle. It is suggested that these granules are probably centrosomes. The chromosome number here is questionable. Although some figures would suggest that four is the haploid number (fig. 5), others would seem to indicate that it may be as high as six. As the telophase stage is reached, the figure is marked by the persistent spindle which extends between the two groups of chromosomes at the poles, and by the presence of a granule in the cytoplasm adjacent to it (fig. 6). This granule is thought to be the remains of the nucleolus. With the exception of one figure in which the spindle appeared to be in a more or less transverse position, spindles in the first division were found to extend longitudinally in the ascus.

After this first division has been completed, two nuclei which appear to be about one-fourth as large as the primary nucleus are formed. Although there is decidedly less chromatin visible, the same beaded effect mentioned above is again in evidence here (fig. 7). The second division was observed

Explanation of Figures 1–11

(All figures were drawn with the aid of an Abbe camera lucida at a magnification of about 1740 diameters.)

FIG. 1. Crozier showing fusion nucleus in the penultimate cell and the disintegrating terminal cell.

FIG. 2. Young ascus with large primary nucleus in late prophase.

FIGS. 3–4. Stages in first nuclear division showing chromosomes at the mid-plane of the intranuclear spindle. Note the centrosomes at the spindle poles.

FIG. 5. Early anaphase of the first nuclear division.

FIG. 6. Telophase of the first nuclear division showing persistent spindle and remains of the nucleolus.

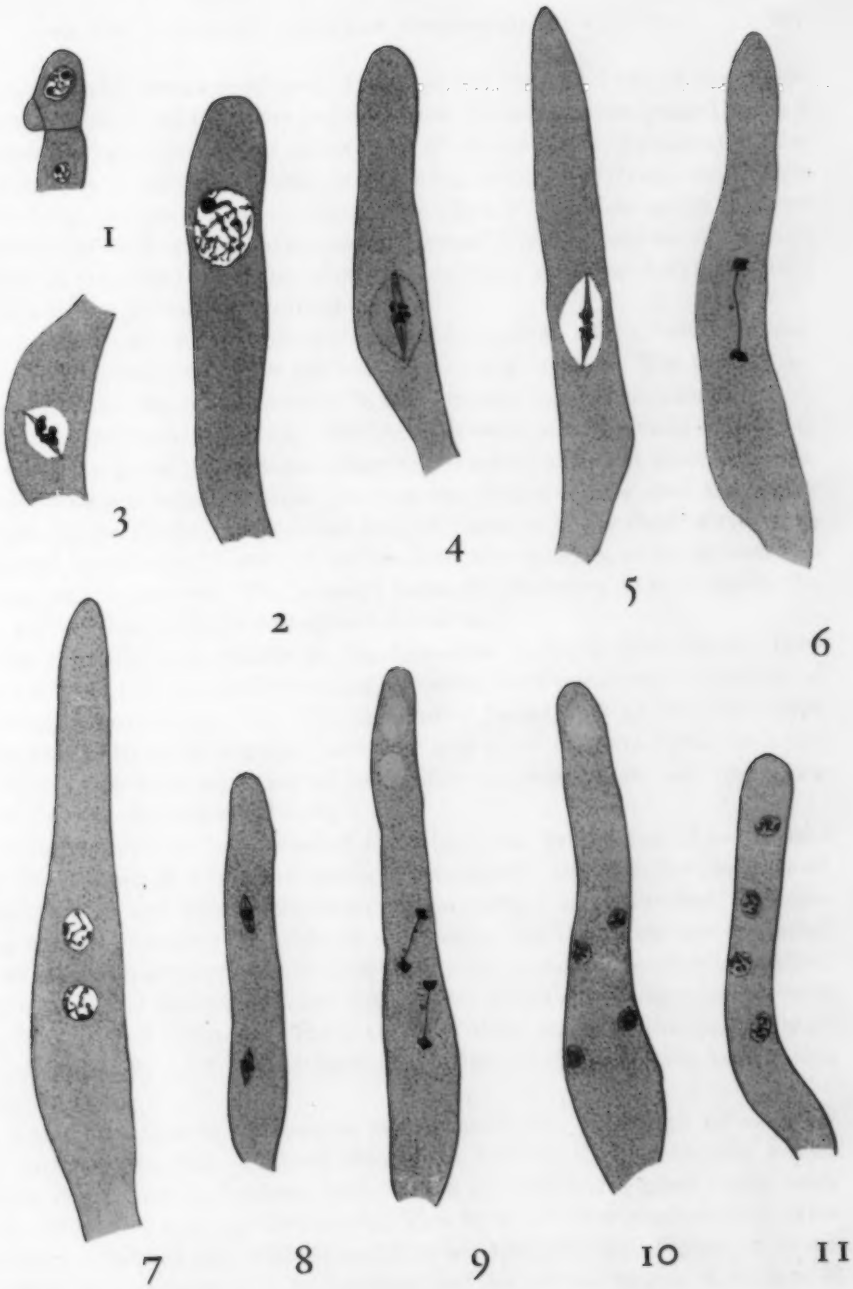
FIG. 7. Binucleate ascus.

FIG. 8. Second division in the ascus at equatorial plate stage.

FIG. 9. Telophase of the second division.

FIG. 10. Newly organized nuclei following completion of the second division.

FIG. 11. Four-nucleate ascus.



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in a considerable number of asci. Although the general form of the figure appeared to be about the same as in the first division, there seemed to be a considerable variation in the orientation of the spindles. Apparently they may take any of three positions in the ascus with equal frequency, being longitudinal, oblique, or nearly transverse (figs. 8–10). Here again it is not possible to be sure of the chromosome number. Figure 9 shows the second division in telophase with the persistent spindles and the darkly-staining granules in the cytoplasm beside them.

Four nuclei are formed after this second division, and a further reduction in size as compared with the binucleate ascus is noted. The beaded appearance of the chromatic network is still present but not so conspicuously as in the larger nuclei (fig. 11). The third division was the most difficult to find, which suggests that it takes place very rapidly and that there is a comparatively short lapse of time between the four-nucleate and the eight-nucleate stages. Spindle orientation is most variable in the third division, as evidenced by figures 12 and 13, which show the spindles as being vertical, oblique, and transverse. The general form of the figure here is again the same as that described for the earlier divisions.

The third division results in the formation of eight free nuclei. They were observed many times occupying a position in a line down the middle of the long, narrow ascus (fig. 15). Asci were found that showed the eight nuclei in a peripheral position, probably just prior to spore formation. The nuclei are somewhat smaller than in the four-nucleate stage, and they show a less definite chromatic network.

From the preparations studied little that was definite could be learned as to the manner in which the spores are delimited, although the presence of beaked nuclei and astral radiations was suggested in a few asci. The sections studied likewise gave evidence suggesting that the spores are delimited as rounded structures which later elongate. Crushed perithecia stained with cotton-blue also showed asci with spores whose shape supports the idea that they are cut out round. The scarcity of these stages in the sections may be attributed in part to the very short time that the spores retain this spherical shape.

When first formed, the spores are uninucleate. Although no satisfactory preparation was obtained showing a nuclear division in the young spores, it can not be doubted that such a division takes place, since each spore ultimately contains two nuclei. This division takes place shortly after the spore is formed and while it is still somewhat spherical. Figure 16 shows an ascus that contains both uninucleate and binucleate spores. A septum is barely discernible in the apical spore. This ascus is noteworthy from two other standpoints. First, it illustrates the fact that the two cells of the spore are approximately equal in size when first formed. Second, it shows that the spores while still unelongated may come to lie side by side. When they again

become uniseriate it is possible that changes from the original serial order may occur. It would seem likely that spores that lie beside each other would either resume their original positions when the ascus elongates or else exchange their original positions. In the ascus shown in figure 16 it appears that sister spores do not lie beside each other, and if the original position were exchanged this fact would be detectable by culturing the spores in their serial order and studying the characters of the isolates. In the ascus shown in figure 18, however, it would appear that sister spores do lie beside each other, and no significance would attach to their possible exchange of position because they are identical twins.

The further elongation of the spores, and the unequal growth in size of the two cells of each spore, which is characteristic of this genus, are the next changes to be observed in the development of the ascus (figs. 17–18). The spores at this time stain more darkly, and a heavier wall begins to be formed. They usually come to fill the greater portion of the ascus, which has grown to keep pace with the enlarging spores. By the time the ascus is mature most of the epiplasm has disappeared and the ascus wall stains faintly. The mature spores, which average 12–15 μ in length, have a heavy, olivaceous wall.

The Mycelium. An investigation of the cytology of the mycelium was accomplished by the preparation of stained microtome sections of fixed blocks of an agar medium upon and through which the fungus had grown. It was found to be branching, septate, and composed of uninucleate cells (fig. 19). Although there was considerable variation in the cells, both as to length and width, no cell of the mycelium was ever found to contain more than one nucleus.

The Conidiophore and the Conidium. Fresh apple leaves parasitized by *Venturia inaequalis* were collected in September of 1939. Slides which revealed the cytological structure of both the conidia and the conidiophores were prepared by scraping portions of the conidial mats from the leaves into a drop of egg albumen on a slide, adding a small drop of fixative, drying,

Explanation of Figures 12–22

FIGS. 12–13. Equatorial plate and telophase stages of the third division. Note irregularity in spindle orientation.

FIG. 14. Stage following completion of the third nuclear division.

FIG. 15. Eight-nucleate ascus.

FIG. 16. Ascus containing both uninucleate and binucleate spores. Note septum in the apical spore.

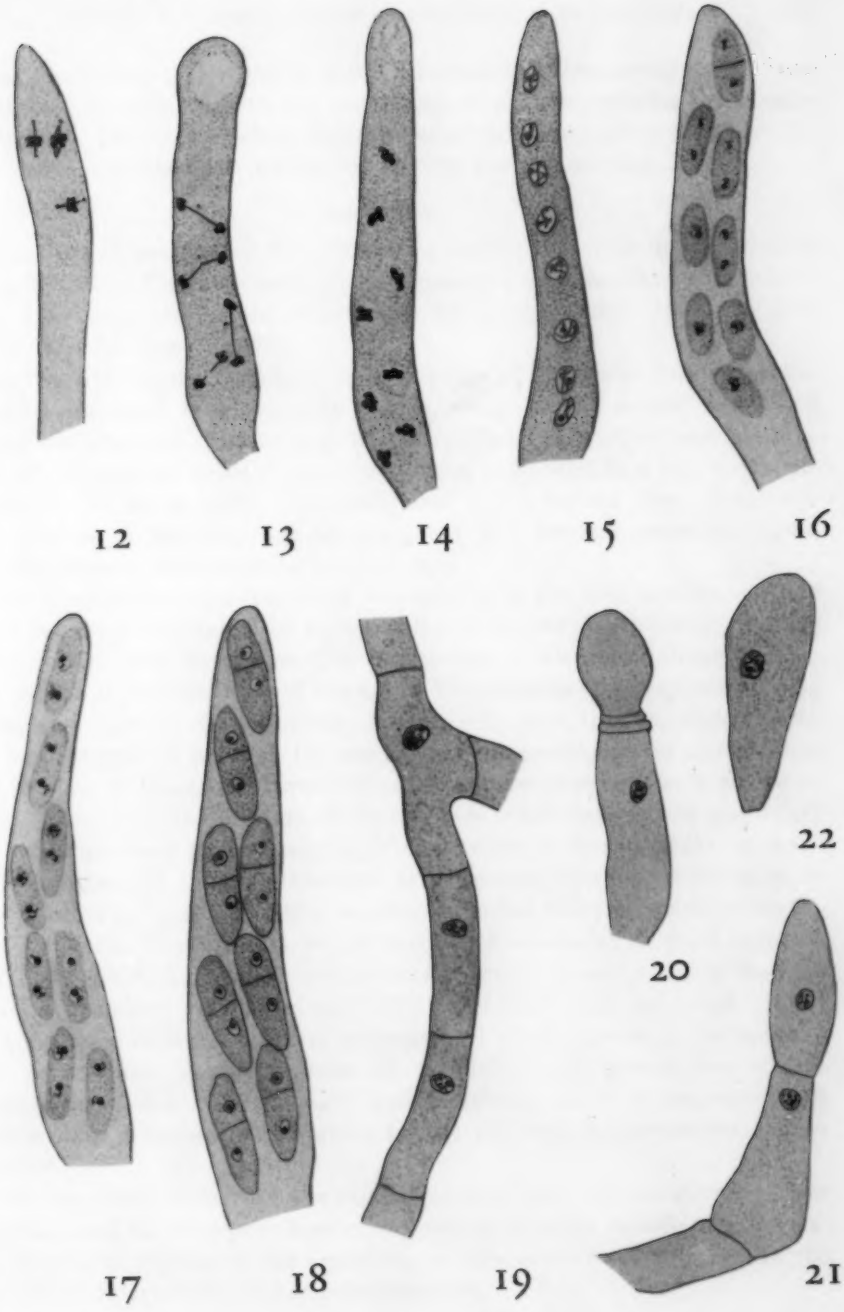
FIG. 17. Ascus showing slightly elongated binucleate spores prior to septation.

FIG. 18. Ascus with spores elongated, septate, and showing beginnings of uneven growth of the two cells.

FIG. 19. Mycelium showing uninucleate cells.

FIGS. 20–21. Conidia and conidiophores with uninucleate cells.

FIG. 22. Uninucleate conidium.



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rinsing in water, and staining with Heidenhain's haematoxylin. It was found that the cells of both the conidiophores and the conidia are always uninucleate. The nuclei, which are comparatively large, show a rather distinct chromatin reticulum within the nuclear membrane (figs. 20–22).

DISCUSSION

Relations of position of the spindles in nuclear divisions in the ascus to the serial order of arrangement of the ascospores and phenomena of inheritance have been studied in *Neurospora* by Dodge (1927, 1936), Wilcox (1928), and Lindegren (1932).

In the first nuclear division in the ascus of *Venturia inaequalis* the spindle is oriented longitudinally in the ascus. In the second and third nuclear divisions the spindles may be longitudinal, oblique, or nearly transverse. Following the third division the nuclei are found in a line down the middle of the ascus. After the ascospores are delimited they frequently show a more or less biseriate arrangement, but become uniseriate again when the ascus elongates prior to dehiscence.

The longitudinal orientation of the spindle in the first nuclear division places the daughter nuclei in such position that, barring nuclear or spore migration, the four ascospores that derive their nuclear complements from each will lie at opposite ends of the ascus. The position of the spindles in the second and third nuclear divisions is ordinarily such that the sister nuclei will be arranged in pairs in the serial order of occurrence of nuclei from base to apex of the ascus. However, an ascus was observed, as is shown in figure 13, in which the position of the spindles would suggest the possibility of a departure from perfect pairing. Furthermore, in asci in which the ascospores temporarily assume a biseriate arrangement, there would seem to be some possibility for change from the original serial order of spores when the ascus elongates. These results, which have much similarity to those reported by Wilcox (1928) for *Neurospora sitophila*, are in accord with the findings of Keitt, Palmiter, and Langford (1938) and Keitt and Langford (1940) on the relation of serial order of arrangement of the spores in the ascus to their inheritance. Further studies of variability and inheritance of this organism are being made by Keitt and Langford, and it is projected that these will be discussed in relation to the cytological phenomena herein reported.

The fact that the cells of the vegetative mycelium, the conidiophore, the conidium, and the ascospore are uninucleate is of much significance in relation to genetic studies of this organism, as this would seem to preclude the possibility of variability due to heterocaryosis.

SUMMARY

The asci of *Venturia inaequalis* arise from croziers near the base of the ascocarp. The primary ascus nucleus is large and shows prominent chro-

matin beads. Three successive nuclear divisions in the ascus result in the formation of eight nuclei. The spindles in the first division are oriented longitudinally in the ascus, while those of the second and third are longitudinal, oblique, or nearly transverse. The position of the spindles is such that after each division the sister nuclei ordinarily are arranged in pairs in the serial order of occurrence of the nuclei from base to apex of the ascus. Barring nuclear or spore migration, the four spores in either end of the ascus should ordinarily derive their nuclear complements from one first-division nucleus. It appears that sister spores ordinarily lie next to each other in the ascus. The spores seem to be delimited as spherical structures. They are at first uninucleate, but a nuclear division followed by a cell division soon occurs and each spore is then composed of two uninucleate cells of equal size. The spores then elongate rapidly, the two cells of each growing unequally. The cells of the vegetative mycelium, the conidiophore, and the conidium are uninucleate.

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A NOTE ON SAPIUM

JOSEPH MONACHINO

During the course of routine identification work in the herbarium of the New York Botanical Garden some studies were undertaken on a certain group of the genus *Sapium*. These studies have revealed the desirability of transferring three specific names to varietal rank, and have brought to light a hitherto undescribed variety.

SAPIUM BIGLANDULOSUM (Aubl.) Müll.-Arg. var. **nitidum** Monachino, var. nov. Haec varietas a forma typica speciei recedit foliis manifeste alternis nitidis obovatis usque ad ellipticis integris, ad apicem complanatis; glandis petiolorum brevibus, in petiolo sitis; spicis singulis terminalibus tenuibus elongatis; capsulis pedicellatis glabris.

This variety differs from the typical form of the species in its leaves being manifestly alternate, shining, obovate to elliptic, entire, with flat tips; petiolar-glands short, on the petioles; spikes single, terminal, slender, elongated; capsules pedicellate, smooth.

Stipules small, ovate to oblong, acutish or blunt at apex; petioles slender, 1–3.5 cm. long, their glands borne at the apex, short; leaf-blades shining when mature, obovate to oblanceolate or elliptic, 3–13 cm. long, 1.5–5 cm. wide, acute at base, extending down the petiole and becoming sulcate between the glands, typically short-acuminate and blunt (or merely rounded) at the apex, without a reflexed or unguliform acumen; prominent primary veins relatively few and distant (6–15), curved and running parallel with the leaf-margins; edge of leaf-blade with a narrow cartilaginous rim, entire (in the type); staminate spikes solitary, terminal, slender, up to 15 cm. long; glands on the rachis long and narrowly oblong, with their ends curving upwards from the rachis or raised; capsules distinctly pedicellate (the pedicels 2–4 mm. long), smooth, up to 8 mm. long and wide, composed of 2 cocci (in the type), 2-valved, each valve splitting again about ¾ of the distance to the base, with thin edges, the cell-partitions remaining on the central axis after dehiscence; seeds about 6 mm. long and wide, coated with a red pseudo-aril.

BRITISH HONDURAS: on deep river-alluvium, Santa Rosa Pasture, 2 miles from El Cayo, alt. 65 m., *J. B. Kinloch 340*, May 28, 1940, TYPE; in the Britton Herbarium of the New York Botanical Garden.

Kinloch gives the following additional information about the variety: a common tree in both alluvium and limestone soils, to 60 feet tall; trunk diameter to 24 inches; bark smooth, gray; crown dense and spreading; latex white, rubbery, abundant; with the general habit of *Ficus radula*. The leaves have a dark-green petiole and red-tinged midrib when fresh, their margins crenulate. The fruit is a 2-celled capsule.

Many of the species of the genus *Sapium* are not only extremely variable in themselves, but also approximate closely related species in such an intergrading manner that separate units can be recognized only by the use of

composite characters. Any single diagnostic or "key" character, such as venation, shape, size, and position of petiolar glands, and leaf-apices, or the singularity or plurality of inflorescence-spikes, is far too variable to be categorically accepted as a means for identification. In a plant group of such disposition the author believes that the nomenclatural designation of "variety" is the more modest and accurate designation for the entities or nuclei of complexes, and that a treatment such as that of Müller in De Candolle's *Prodromus*, where the species *S. biglandulosum* is given more than a dozen varieties (and can easily be made to include twice as many), is preferable to the more rigid binomialism of Pax in *Das Pflanzenreich*. Not even Pax could entirely refrain from varietalizing, since, for instance, he recognized nine distinct varieties of *S. marginatum*. Only because of this belief does the present writer relegate the new plant from British Honduras, described above, to varietal rank; for, otherwise, as species in Pax's treatment go, it would certainly merit the status of a separate species.

It is perhaps also worthy of mention that when *Kinloch 340* was entrusted to the writer for identification, the fact that it was a *Sapium* from British Honduras led him to consult Standley & Record's publication on the flora of that country. The only species therein recorded, *S. jamaicense* Sw., is represented in the Britton Herbarium by specimens from Panama, Costa Rica, and Guatemala. Two additional specimens labeled "*Sapium jamaicense*," from Central America, resemble each other closely, but are obviously incorrectly determined. Their leaves have well-developed apical glands. Plate 17 in volume 12 of Contributions from the United States National Herbarium (1908) fits them perfectly. This plate represents SAPIUM BIGLANDULOSUM (Aubl.) Müll.-Arg. var. **oligoneurum** (K. Schum. & Pittier) Monachino, stat. nov. (*Sapium oligoneurum* K. Schum. & Pittier, Contrib. U. S. Nat. Herb. **12**: 168, *pl. 17*. 1908). One of the specimens, from a staminate plant, is from the republic of Honduras; the other (*W. A. Schipp 1049*), a fruiting specimen, is from British Honduras. Its pedicellate capsules and other characters fit the original description of S. BIGLANDULOSUM (Aubl.) Müll.-Arg. var. **sulciferum** (Pittier) Monachino, stat. nov. (*Sapium sulciferum* Pittier, Contrib. U. S. Nat. Herb. **12**: 169, *f. 10*. 1908). On the other hand, in *Das Pflanzenreich*, volume IV, 147[5] (1912), "*S. sulciferum*" is included in the "Clavis specierum" under the heading "A. Capsula sessilis, non stipitata," and Schipp's specimen in that key would come out as SAPIUM BIGLANDULOSUM (Aubl.) Müll.-Arg. var. **bogotense** (Huber) Monachino, stat. nov. (*Sapium bogotense* Huber, Bull. Herb. Boiss. (II) **6**: 355, *f. 13*. 1906). Under the circumstances it is not possible to definitely identify these two specimens and a final statement of their identity must await comparison with the type specimens of the above-mentioned varieties.

THE NEW YORK BOTANICAL GARDEN,
NEW YORK, NEW YORK.

BREEDING WORK TOWARD THE DEVELOPMENT OF A TIMBER TYPE OF BLIGHT-RESISTANT CHESTNUT. REPORT FOR 1939[1]

ARTHUR HARMOUNT GRAVES

The purpose of this work is to develop, by breeding, a type of chestnut tree of tall straight growth, and at the same time, resistant to the blight fungus, *Endothia parasitica* (Murr.) P. J. and H. W. And. It is generally known that this fungus, inadvertently introduced from Asia more than 40 years ago, has now practically exterminated the American chestnut (*Castanea dentata*) at least so far as its value as a forest tree is concerned.

Ten years ago[2] we began breeding the American chestnut with an oriental species, *Castanea crenata*, the Japanese chestnut. That species has considerable resistance to the attack of the blight fungus, but is a comparatively low growing tree, quite unsuitable for replacing the American tree species as a timber tree in our Eastern forests.

In general, the first generation of Japanese-American hybrids has shown dominance of the American species, as evidenced by the erect habit of growth and by the leaf characters. However, the dominance is not complete. This is shown by the fact that the susceptibility to the blight is not so great as that of the American parent. In order to introduce greater resistance into the stock, it has been our policy to cross these Japanese-American hybrids again with resistant Japanese and with resistant Chinese, with the result that we now have 93 trees of (*C. crenata* × *C. dentata*) × *C. crenata* or the reciprocal, and 8 of (*C. crenata* × *C. dentata*) × *C. mollissima*, growing on our plantation. We have also intercrossed these F_1's (*C. crenata* × *C. dentata*) in the hope of developing forms with a greater content of Japanese stock. At present we have 139 of these F_2's. Many other crosses have been made (see table 2) and representatives of most of these are now growing on the trial grounds, where they are being tested for disease resistance by our inoculation method. These are located at the eastern end of the Sleeping Giant Mountain, Hamden, Connecticut.

Cooperative Planting. In 1939 we continued to extend our cooperative plantations, and accordingly supplied seedlings to Dr. D. F. Jones, of the Connecticut Agricultural Experiment Station at New Haven, for planting on the experimental farm of the Station at Mt. Carmel, Hamden, Conn.

[1] Brooklyn Botanic Garden Contribution No. 92.

[2] Recent annual reports have been published in the Brooklyn Botanic Garden Record as follows. For 1929, Brooklyn Botanic Garden Record **19**: 62–67; for 1930, **20**: 83–87; for 1931, **21**: 46–53; for 1932, **22**: 57–63; for 1933, **23**: 67–75; for 1934, **24**: 59–65; for 1935, **25**: 62–75; for 1936, **26**: 47–60; for 1937, **27**: 44–55; for 1938, **28**: 54–60; for 1939, **29**: 58–63.

The trees now growing here, as well as in the two other cooperative plantations already established, are shown in table 1.

TABLE 1. COOPERATIVE PLANTATIONS

Cooperative Plantation No. 1

On Farm of Dr. W. W. Herrick, Sharon, Conn.
Seedlings in first year of growth; from nuts harvested in 1938

C. crenata × *C. dentata*	2
C. crenata × (*C* × *D*)[1]	10
(*C* × *D*) × *C. crenata*	3
(*C* × *D*) × (*C* × *D*)	8
C. mollissima × *C. dentata*	2
C. mollissima × (*C* × *D*)	14
C. Seguinii × *C. crenata*	1
S8 × *C. dentata*	4
S8 × *C. mollissima*	6
S8 (from open pollination) 2 years old	75
Total	125

Cooperative Plantation No. 2

On Grounds of New Haven Water Company, Orange, Conn.
All seedlings in first year of growth; from nuts harvested in 1938

Seedlings from open pollinations	
C. crenata × *C. dentata*	119
Seedlings from controlled pollinations	
C. crenata × (*C* × *D*)	6
C. Seguinii × *C. mollissima*	3
C. mollissima × (*C* × *D*)	1
Total	129

Cooperative Plantation No. 3

On Farm of Connecticut Agricultural Experiment Station; Mt. Carmel (Hamden), Conn.
All seedlings in first year of growth; from nuts harvested in 1938

C. mollissima × *C. crenata*	3
C. mollissima × (*C* × *D*)	3
C. crenata × *C. mollissima*	3
C. crenata × *C. dentata*	7
Total	16

[1] *C* × *D* = *C. crenata* × *C. dentata.*

Hybrids of 1939. The following is a brief account of the chestnut hybridization work in 1939. Since I was absent in England and Scotland during most of the period, the direct supervision of the work was in charge of my assistant, Miss Hester M. Rusk. As has been our practice since 1935, all the cross pollinations were made on trees growing at the plantation at Hamden, Connecticut. In the following list, as is customary, the name of the female parent is given first. The combinations with an asterisk are new to science. The numbers in parentheses at the left of certain combinations correspond with the numbered notes which follow.

(1) Most of these are crosses of our most resistant Japanese with valuable American pollen sent us by Mr. J. C. McDaniel of T.V.A., Norris, Tennessee, and by Mr. H. F. Stoke of the Mountain Nut Co., Roanoke, Virginia.

(2 and 3) Include a large number of crosses with our best Japanese American hybrids and our most resistant Japanese and Chinese individuals —145 nuts in all.

(4) In 1932 I secured nuts of the Spanish chestnut, *C. sativa,* from several European Gardens. The resulting seedlings have been particularly

TABLE 2. HYBRIDS OF 1939

		No. of nuts
(1)	*C. crenata* × *C. dentata*	88
	C. crenata × (*C* × *D*)	130
	**C. crenata* × *C. neglecta*[1]	13
	C. crenata × (*C. mollissima* × *C. Seguinii*)	31
(2)	(*C* × *D*) × *C. crenata*	124
(3)	(*C* × *D*) × *C. mollissima*	21
(4)	*(*C* × *D*) × *C. sativa*	5
	(*C* × *D*) × (*C* × *D*)	21
	S8[2] × *C. crenata*	15
	S8 × *C. mollissima*	16
	S8 × (*C* × *D*)	54
	(*S8* × *C. crenata*) × *C. dentata*	3
	*(*S8* × *C. dentata*) × *C. crenata*	2
	*(*S8* × *C. dentata*) × (*C. crenata* × *C. dentata*)	5
	(*S8* × *C. dentata*) × *S8*	21
	(*C. crenata* × *S8*) × *C. crenata*	21
	**C. dentata* × *C. neglecta*	6
	*(*C. dentata* × *S8*) × *C. crenata*	2
	*(*C. dentata* × *S8*) × *S8*	4
(5)	*C. mollissima* × *C. dentata*	41
	C. mollissima × (*C* × *D*)	29
	C. mollissima × *S8*	3
	**C. mollissima* × (*C. crenata* × *S8*)	10
(6)	**C. mollissima* × [(*C* × *D*) × (*C* × *D*)]	34
	C. mollissima × (*C. mollissima* × *C. dentata*)	7
	*[(*C. mollissima* × *C. pumila*) × *C. dentata*] × *C. crenata*	3
	(*C. mollissima* × *C. Seguinii*) × *C. crenata*	35
	(*C. mollissima* × *C. Seguinii*) × *C. dentata*	12
	**C. Seguinii* × (*C* × *D*)	11
	Total	767

[1] *C. neglecta* is a cross of *C. pumila* and *C. dentata*.

[2] *S8*, one of the Van Fleet hybrids, is apparently a combination of *C. crenata* and *C. pumila*. The "*S8*'s" in our plantation are from open pollinated seedlings of S8. For "*C* × *D*" see note to table 1.

unpromising because (1) they die back in the winter and (2) they proved very susceptible to the blight. On the other hand, the growth has been vigorous, with thicker, stronger, and longer shoots than in any other species. It is on account of this valuable growth character that we are trying to incorporate this stock into our hybrids.

(5) One of our best Chinese crosses with *C. dentata* pollen from a seedling raised by us from a nut planted in 1926. The tree from which this nut came was a large specimen near Portland, Maine. This young seedling American, however, is now badly blighted.

(6) A cross of two Japanese American hybrids, four years old, made in 1935, bloomed for the first time this year and was crossed with one of our best Chinese. This, therefore, represents the beginning of the third generation in a time interval of only eight years, and is particularly important as evidence of the short time required for breeding experiments with the chestnut. *Castanea dentata* blooms at the age of about 12 years, most of the Japanese forms at about 5 years. We have heard of Chinese individuals blooming at the age of one year. We have had hybrids blooming and bearing nuts in their first year!

Testing for Disease Resistance by Inoculation with Endothia. This method, begun in 1936, was not continued last year on account of my absence in Europe, but may be resumed in 1940. By inoculation in the past, we have learned what are the most desirable individuals to use for breeding work, from the point of view of disease resistance. The method in use has already been described.[3]

[3] Report of the 28th Annual Meeting of the Northern Nut Growers Association, 1938: 97.

Hybrid Combinations New to Science. In the progress of this cross pollination from year to year new hybrids have been developed. It is our purpose, as soon as all the floral characters appear, to publish descriptions of the more important of these.

The following is merely a list of the new hybrids, a revision of that published early in 1939,[4] and includes the new combinations made by us in 1939.

TABLE 3. NEW CHESTNUT HYBRIDS OF THE BROOKLYN BOTANIC GARDEN 1934–1939

Castanea crenata × *C. neglecta*—1939
(*C* × *D*[1]) × *C. dentata*—1934
[1] See note to table 1.
(*C* × *D*) × *C. mollissima*—1935
(*C* × *D*) × *C. sativa*—1939
(*C* × *D*) × *C. Seguinii*—1936
(*C* × *D*) × *S8*[2]—1936
[2] See note 2 to table 2.
(*C* × *D*) × (*C. mollissima* × *C. Seguinii*)—1937
(*C* × *D*) × (*S8* × *C. dentata*)—1938
S8 × *C. sativa*—1937
S8 × (*C* × *D*)—1936
S8 × (*C. crenata* × *S8*)—1937
(*S8* × *C. crenata*) × *C. dentata*—1938
(*S8* × *C. crenata*) × *C. mollissima*—1938
(*S8* × *C. dentata*) × *C. crenata*—1939
(*S8* × *C. dentata*) × (*C. crenata* × *C. dentata*)—1939
(*S8* × *C. dentata*) × (*S8* × *C. dentata*)—1938
C. dentata × *C. neglecta*—1939
(*C. dentata* × *S8*) × *C. crenata*—1939
(*C. dentata* × *S8*) × *S8*—1939
C. mollissima × (*C* × *D*)—1935
C. mollissima × (*C. crenata* × *S8*)—1939
C. mollissima × [(*C* × *D*) × (*C* × *D*)]—1939
(*C. mollissima* × *C. crenata*) × *C. sativa*—1937
(*C. mollissima* × *C. pumila*) × *C. dentata*—1934
[(*C. mollissima* × *C. pumila*) × *C. dentata*] × *C. crenata*—1939
[(*C. mollissima* × *C. pumila*) × *C. dentata*] × (*C* × *D*)—1938
(*C. mollissima* × *C. Seguinii*) × *C. crenata*—1937
(*C. mollissima* × *C. Seguinii*) × *C. dentata*—1938
(*C. mollissima* × *C. Seguinii*) × *C. sativa*—1937
(*C. mollissima* × *C. Seguinii*) × (*C* × *D*)—1937
(*C. mollissima* × *C. Seguinii*) × (*C. mollissima* × *C. Seguinii*)—1937
C. Seguinii × *C. alabamensis*—1938
C. Seguinii × *C. dentata*—1937
C. Seguinii × *C. pumila*—1937
C. Seguinii × *C. sativa*—1937
C. Seguinii × (*C* × *D*)—1939

The following list of trees growing at the trial grounds at Hamden is presented to show not only what forms we now have under cultivation, but also, as indicated by the numbers at the right, the relative importance accorded to each species, variety or hybrid. For instance, *Castanea dentata*, the American chestnut, is represented by 100 trees, which have been grown from nuts sent us from many states throughout the range of the chestnut, from Maine to North Carolina. Different degrees of disease resistance occur in different strains and even individuals of *Castanea*. For this reason nuts of the American chestnut are much desired for planting. Without going into further detail, we let the list speak for itself.

Acknowledgments. As noted in the report of the work last year, the American Association for the Advancement of Science, in December, 1938, awarded us a grant-in-aid for the continuance of the work during 1939.

[4] Since the publication of this list in 1939, we have had access to unpublished records of the U. S. Department of Agriculture, and find that some of the combinations published by us as new had already been made by the Division of Forest Pathology, U.S.D.A.

TABLE 4. CHESTNUT SPECIES, VARIETIES, AND HYBRIDS GROWING AT HAMDEN, CONNECTICUT OCTOBER, 1939

Name	*Number of Trees*
Castanea alnifolia—Alder-leaved Chinquapin	4
C. Ashei—Ashe Chinquapin	2
C. crenata—Japanese Chestnut	53
C. dentata—American Chestnut	100
C. Henryi—Chinese Timber Chinquapin	13
C. Margaretta	1
C. mollissima—Hairy Chinese Chestnut	96
C. mollissima Mammoth—Chinese Chestnut var.	1
C. ozarkensis—Ozark Chinquapin	11
C. pumila—Chinquapin	32
C. sativa—Spanish Chestnut	55
C. Seguinii—Chinese Dwarf Chinquapin	16
**S8* (*C. crenata* × *C. pumila*)	2
C. crenata × *C. dentata*	78
C. crenata × *C. mollissima*	6
C. crenata × *S8*	5
C. crenata × (*C* × *D*)	43
(*C* × *D*) × *C. crenata*	50
(*C* × *D*) × *C. dentata*	11
(*C* × *D*) × *C. mollissima*	8
(*C* × *D*) × (*C* × *D*)	139
(*C* × *D*) × (*C. mollissima* × *C. Seguinii*)	1
(*C. crenata* × *S8*) × (*C. crenata* × *S8*)	1
C. dentata × *C. mollissima*	12
C. dentata × *S8*	10
C. mollissima × *C. crenata*	2
C. mollissima × *C. dentata*	57
C. mollissima Mammoth × *C. dentata*	8
C. mollissima × *C. pumila*	1
C. mollissima × *C. Seguinii*	4
C. mollissima × *S8*	7
C. mollissima × (*C. crenata* × *C. dentata*)	152
C. mollissima Mammoth × (*C. crenata* × *C. dentata*)	8
(*C. mollissima* × *C. crenata*) × *C. sativa*	1
(*C. mollissima* × *C. pumila*) × *C. dentata*	7
(*C. mollissima* × *C. Seguinii*) × *C. crenata*	4
(*C. mollissima* × *C. Seguinii*) × *C. mollissima*	3
(*C. mollissima* × *C. Seguinii*) × *C. sativa*	1
(*C. mollissima* × *C. Seguinii*) × (*C. mollissima* × *C. Seguinii*)	2
(*C. mollissima* × *C. Seguinii*) × [*C. sativa* × (*C* × *D*)]	1
C. Seguinii × *C. alabamensis*	3
C. Seguinii × *C. crenata*	1
C. Seguinii × (*S8* × *C. dentata*)	1
S8 × *C. crenata*	7
S8 × *C. dentata*	20
S8 × *C. mollissima*	30
S8 × *C. sativa*	16
S8 × *C. Seguinii*	9
S8 × (*C. crenata* × *C. dentata*)	3
(*S8* × *C. crenata*) × *C. dentata*	11
(*S8* × *C. dentata*) × (*C. mollissima* × *C. dentata*)	4
Stoke Hybrid No. 1, grafted on *C. mollissima*	2
Stoke Hybrid No. 1, grafted on *C. crenata*	2
Stoke Hybrid No. 2, grafted on *C. mollissima*	3
Stoke Hybrid No. 2, grafted on *C. crenata*	1
Stoke Hybrid No. 3, grafted on *C. mollissima*	2
Stoke Hybrid No. 4, grafted on *C. mollissima*	2
Various seedlings from "open pollinations"	54
Chinese and Japanese seedlings from open pollinations (approximately)	750
Total	1929

We acknowledge with pleasure the continued cordial cooperation of the Division of Forest Pathology, Bureau of Plant Industry, Washington, D. C. Many institutions and individuals, e.g., the Garden Club of America and the Connecticut Forest and Park Association, have granted us valuable assistance with offers of land for additional plantings and by sending us pollen and nuts of various species. A list of the donors of pollen and nuts is printed in the Annual Report for 1939 of the Brooklyn Botanic Garden, pages 56–59.

BROOKLYN BOTANIC GARDEN,
BROOKLYN, NEW YORK.

A REVISION OF "LAURENTIA" AND ALLIED GENERA IN NORTH AMERICA

ROGERS MCVAUGH

The genus *Laurentia* (Campanulaceae, Lobelioideae) was founded by Petro Antonio Micheli in 1729,[1] and included the single species known to him, a native of the Mediterranean region, the plant now called *L. Michelii* A. DC. Numerous other species have been described from southern Europe, tropical and subtropical Africa, western United States, Mexico, the West Indies, and Australia. At the present time there is considerable confusion as to the generic limits and as to the distinctions between *Laurentia* and related genera.

The genus *Laurentia*, as originally understood, and as delimited by authors generally as late as the publication of Bentham and Hooker's *Genera Plantarum* (1876), included a group of herbaceous, blue-flowered species with the corolla-tube lacking the dorsal slit that characterizes the genus *Lobelia*, with the ovary almost or wholly inferior, and with the filaments usually loosely adherent to the corolla-tube. The character that separates this genus from *Lobelia* is that the corolla in *Laurentia* is not at all divided on the side between the two narrow dorsal lobes, while in *Lobelia* it is slit to the base or very nearly so. Such a character appears to be scarcely of generic value, even in the Lobelioideae, where there prevails such uniformity of floral structure that no other sort of character is available.

Professor F. E. Wimmer of Vienna, the greatest living authority on the Lobelioideae, states[2] that the group as a whole contains about 1,000 species, distributed among 23 genera. Of these more than 800 belong to the four genera, *Burmeistera*, *Centropogon*, *Siphocampylus*, and *Lobelia*. Among all these 23 genera and 1,000 species, there are a few only that are separated by strong morphological characters; *Downingia*, for example, has the capsule dehiscent by lateral slits instead of by apical valves, and is quite distinct from all other genera. Another example is *Lysipomia*, an Andean genus of about 15 species, in which the capsule opens by an operculum. The number and disposition of the floral parts are identical in all the species of the subfamily, save those mentioned above and a few others. The taxonomist, as a consequence, has to fall back on relative characters such as the thickness or fleshiness of the hypanthium or the depth of the sinuses of the corolla. Such characters, while fairly satisfactory in any given small geographic area or when a small number of species is under consideration, usually break down

[1] Nov. Gen. Pl. t. 14. 1729.

[2] Campanulaceae, in Macbride, Flora of Peru. Field Mus. Publ. Bot. 13 (6): 383–489. 1937.

when applied to large series of species from all parts of the earth. As Gleason has pointed out[3] it would be perfectly feasible to unite the genera *Burmeistera*, *Centropogon*, and *Siphocampylus* into one vast genus without overstepping the bounds of logic. It would be equally possible to add to this genus the present genera *Lobelia*, *Laurentia*, and *Isotoma*. The principal objection to such a course is, in my opinion, a practical one. The limits of genera of the sort here considered are determined by convention and usage as well as by severe logic. The name-changes involved in such a step as that discussed above would be many, and much confusion and unnecessary synonymy would result.

It appears, then, that almost any attempt at a natural classification of the Lobelioideae must strike a balance among the following courses: (1) Define a considerable number of small genera, each fairly uniform in character, but set off from closely related groups by purely arbitrary characters. This course involves the creation of a number of new names. (2) Make generic limits ample enough to allow for the inclusion of most of the anomalous species. This will tend to make the genera larger and fewer, and will also necessitate the creation of many new names. (3) Make the genera as small and homogeneous as is compatible with logic, at the same time recognizing the weight of convention as it bears on the subject of generic limits. It seems to me that best results may be obtained from this last course, if at the same time it be remembered that the "genus", *as ordinarily defined*, is a conventional concept; it is less a natural unit than the species and more to be thought of as a means of classification. Convenience, therefore, must be taken into account as well as apparent kinship between species or groups. A single example will serve to illustrate this point. The plant known as *Lobelia laxiflora*, which is widespread in Mexico and Central America, is, I think, much more closely akin to numerous South American species of *Siphocampylus* than it is to the rest of the genus *Lobelia*. Because of its slit corolla-tube, however, it has been assigned without hesitation to *Lobelia* by most botanists. To transfer it to *Siphocampylus*, regardless of the possible theoretical value of such a course, would not only confuse the nomenclature but would necessitate the revision of the generic limits of *Siphocampylus* to an undue degree and would tend to break down the already somewhat nebulous distinction between it and *Lobelia*. An adequate revision of the generic characters of *Lobelia* and *Siphocampylus* is greatly to be desired. The genera in question, while apparently good natural groups, have been so arbitrarily separated in the past that their truly definitive characters, if any, have been obscured.

When subjected to critical examination, the characters that separate *Laurentia* and *Isotoma* from the large genus *Lobelia* are seen to break down

[3] Studies on the flora of northern South America—IV. The genus *Burmeistera*. Bull. Torrey Club 52: 93–104. 1925.

entirely. The principal character, the presence or absence of a dorsal slit or cleft in the corolla-tube, is of no real value as an indicator of generic differences. Many species of *Lobelia*, closely related otherwise to North American species, have the cleft extending only part way to the base, usually three-fourths of the distance or more. The only species of *Lobelia* native to southern Europe, *L. urens*, has the tube cleft almost exactly halfway, while the little-known *L. sinaloae*, of western Mexico, lacks the cleft entirely. The last-mentioned species, is, therefore, a *Laurentia* by morphological standards, but is so closely related to *Lobelia Hartwegi* as to be scarcely distinguishable from that species except by the single feature of the corolla-tube.

The adherence of the filaments to the corolla-tube is also a variable feature throughout the Lobelioideae, varying roughly in accordance with the depth of the dorsal cleft of the corolla-tube. In general, the filaments are more likely to be adnate to the corolla in species having the corolla-tube without a dorsal cleft, but the degree of adherence is variable and no sharp line can be drawn between the species having free stamens and those with stamens adherent to the corolla.

It is proposed, therefore, to unite with the widespread genus *Lobelia* the two somewhat localized groups previously known as *Laurentia* and *Isotoma*. The latter is entirely Australian, and appears to differ from the former in no way except that in some species the three lower corolla-lobes are scarcely broader than the two upper ones, which makes the limb of the corolla appear almost regular. *Isotoma* was originally proposed by Robert Brown[4] as a section of *Lobelia*, and this section may now be taken to include the southern European, African and North American species described under *Laurentia* (except as mentioned below), and the Australian species described under *Isotoma* as a genus. Such a concept of generic limits will necessitate the formation of a very few if any new names, since most of the species concerned have already been given names in the genus *Lobelia*.

It seems to me that one cannot logically maintain genera which are widely distributed, the species of which differ from the species of other widespread genera by trivial and inconstant characters, so that the supposed genera have to be separated by purely mechanical analysis. If genera are actual phylogenetic units they will inevitably be small and homogeneous (and ordinarily not of wide geographical distribution), or large and relatively heterogeneous, usually widespread in space, with similar variants appearing in different parts of the range, the variants never wholly separable from each other nor from the original genus. The small and homogeneous genera just mentioned are mostly recognizable by some striking combination of characters, while such artificial genera as *Laurentia* are not definable except in the most arbitrary fashion.

[4] Prodr. Fl. Nov. Holl. 565. 1810.

Such definition of generic limits appears to be a natural consequence of organic evolution. A genus may be expected to be in the process of evolution, in which case we should expect it to be relatively small and poorly differentiated from related groups, or it may be well-established and widespread, fairly homogeneous and wholly distinct from all related groups.

In view of such reasoning either *Laurentia* or *Isotoma* may be thought of as a concept rather than as an actual assemblage of species. The European, African, Australian, and American members of either "genus" are not more closely related to each other than to species of the large group *Lobelia* and, accordingly, it seems best to consider them all as species of a single genus, but perhaps as belonging to local manifestations of that genus. The Lobelioideae as a whole are almost certainly an ancient group, but evolution in some parts of the subfamily appears still to be active. In the future such localized phases of large genera may be recognized as genera, but at present they appear to be insufficiently distinct to justify such a course.

There are in North America several very diverse species and species-groups which have been, in the past, arbitrarily assigned to the genus *Laurentia*, or to *Isotoma*. One of these species (*Laurentia* or *Isotoma longiflora*) seemingly has its closest relative in the Hawaiian genus *Brighamia*, and apparently should be taken as the type species of a monotypic genus. Secondly, a group of 5 or 6 closely related species in Mexico and Central America forms a natural genus very near to some Mexican species of *Lobelia*. This group appears distinct from other genera by several characters of habit, flower and fruit, and is typified by *Diastatea virgata* Scheidw. (*Lobelia ramosissima* Mart. & Gal.). Finally, a single species in the Rocky Mountain region, and a second species ranging from California to Baja California have been included in *Laurentia*. The former seems to be generically distinct (*Porterella carnosula* (H. & A.) Torr.) and the latter, if not generically distinct, may be assigned to *Lobelia* (*Palmerella debilis* A. Gray; *Laurentia debilis* McVaugh).

The following key will serve to set forth the characters of the genera just discussed:

1. Corolla pure white, salverform, the tube narrowly cylindric, 50–135 mm. long, the lobes subequal; pedicels each with a pair of filiform bracteoles, 2–4 mm. in length, at or near the base; ovary inferior or very nearly so, the apex inclosed by the free rim of the hypanthium; seeds conspicuously foveolate-reticulate ..... 1. *Hippobroma*

1. Corolla blue or purplish, sometimes pale, strongly bilabiate, three of the lobes much broader than the other two; flower, including hypanthium, 25 mm. long or less; pedicels ebracteolate; seeds smooth, lustrous 2

2. Ovary inferior or essentially so; corolla withering after anthesis, not enlarged in fruit 3

3. Corolla-tube 3.5–6.0 mm. long; plants wholly glabrous; foliage-leaves very nar-

rowly linear or rarely lanceolate, entire, rarely more than 2.0 mm. wide; flower-bracts mostly broader than the leaves; seeds fusiform, dark-apiculate.
4. *Porterella*

3. Corolla-tube 9.0–18.0 mm. long; plants bristly-pubescent above, at least on the corolla-tube; foliage-leaves broader, serrate, the middle and upper ones rarely less than 2.5 mm. wide, and the lower ones rarely less than 5.0 mm. wide; flower-bracts narrower than the leaves; seeds ellipsoid-lenticular, with rounded ends.
3. *Lobelia* § *Isotoma*

2. Ovary superior or attached to hypanthium at very base only; corolla much distended by the developing capsule and becoming at length scarious and hyaline.
2. *Diastatea*

1. Hippobroma G. Don, Gen. Syst. 3: 717. 1834.

Lobelia, sect. *Solenanthis* Kunth, HBK. Nov. Gen. & Sp. 3: 309. 1819. *Isotoma*, sect. *Solenanthis* A.DC., DC. Prodr. 7: 412. 1839. TYPE SPECIES: *H. longiflora* Don, *l.c.*

Stems coarse, with acrid, milky, poisonous juice, erect or decumbent, to 7 mm. in diameter at base, simple or with a few subordinate side branches, pubescent at least above, or nearly glabrous, pale yellow-green, 15–50 (90) cm. high. Cauline leaves from few to 25, spreading or ascending, membranous, pubescent on the veins and on the lower surface or almost glabrous, said to be dull blue-green above and glossy gray-green beneath. Blades elliptic to oblanceolate, coarsely repand-dentate and minutely callose-denticulate on the margin, narrowed abruptly to the obtuse or acutish mucronulate apex and drawn out slowly to the narrow subpetiolar decurrent base. Size of blade 2.5–6.0 × 10–24 cm., usually 3–4 times as long as wide. Roots somewhat fleshy (woody?); perennial?

Flowers 8–35 in the axils of the upper leaves, the "inflorescence" 6–26 cm. long and comprising half to two-thirds the height of the entire plant or even more. Pedicels more or less upright in flower (declined in fruit), 7–15 mm. long in fruit, about 1 mm. in diameter, short-hirsute, each normally with a pair of filiform bracteoles, 2–4 mm. in length, at or near the base.

Hypanthium in anthesis turbinate, sparsely short-hirsute, becoming ellipsoid or ellipsoid-campanulate in fruit, 7–9 mm. in diameter. Capsule ¾ inferior or more, often appearing wholly inferior because closely invested by the free rim of the hypanthium. Capsule pendent when mature, dehiscing loculicidally by two apical valves. Calyx-lobes narrowly linear, 1 mm. wide by 10–22 mm. long, callose-denticulate on the margins, ciliate or nearly glabrous.

Flower 80–160 mm. long, including hypanthium. Corolla salverform, pure white, slightly fragrant, puberulent except on the inner side of the lobes. Tube entire, narrowly cylindric, 50–135 mm. long, 1.0–2.5 mm. in diameter. Lobes subequal, spreading, 3–10 mm. wide by 13–27 mm. long. Filaments 58–95 mm. long, equalling or somewhat exceeding the corolla-tube, connate by their edges (or exceptionally free) at apex, adnate to the corolla-tube and free from each other from base to a point just below the apex of the tube. Anther-tube 5–6 mm. long by about 2 mm. in diameter, the orifice oblique and not closed by the three longer anthers; all anthers white-bearded at extreme tip, the two shorter ones densely tufted.

Seeds ellipsoid or cylindric with rounded ends, 0.6–0.8 mm. long, light brown, minutely and regularly foveolate-reticulate.

A single species, with characters of the genus:

1. HIPPOBROMA LONGIFLORA (L.) G. Don, Gen. Syst. **3**: 717. 1834. *Lobelia longiflora* L., Sp. Pl. 930. 1753; Type locality: "Habitat in Jamaica ad ripas." TYPE: Not seen. Linnaeus apparently had no specimen in 1753 and perhaps based his description merely upon Sloane's plate and description of 1707.[5] Rendle[6] states that there is extant a specimen in the Sloane herbarium at the British Museum. This should properly be regarded as the TYPE. *Rapuntium longiflorum* Mill., Dict. ed. 8. 1768. *Isotoma longiflora* Presl, Prodr. Mon. Lob. 42. 1836. *Laurentia longiflora* E. Wimm. in Macbr., Field Mus. Publ. Bot. **13**(6): 474. 1937, non Schlechter, 1922.

River-banks, clearings, fields and waste grounds. Widely distributed as an escape from cultivation in tropical and subtropical regions of both hemispheres. Throughout both Greater and Lesser Antilles. In continental North America extending from Florida (where collected by Rugel) along the Gulf Coast and southward throughout the lowland areas of Mexico and Central America, north on the west coast to Sonora. Rare at elevations of more than 1,000 meters. Flower and fruit throughout the year.

Although now rather widely distributed in the tropics as a weedy species, *Hippobroma longiflora* seems originally to have been confined to the West Indies. The evidence for this is twofold. In the first place, in a very large proportion of the situations where the species now occurs outside the West Indies, it is known to be an escape from cultivation, or is thought by the collector to be an introduced species. Its somewhat weedy nature and the habitats in which it is found tend to add weight to this evidence. In the second place, the species is seemingly becoming more frequent in various parts of tropical America. The early travellers do not mention it from continental America; Kunth[7] lists it from Cuba only; it is not mentioned in Seemann's *Flora of Panama*.[8] Alphonse De Candolle, in the *Prodromus*[9] says merely "in paludosis Caribaeorum." There are collections from Cuba and Puerto Rico in the herbarium of Sessé and Mociño (approximate date 1800), but the species is not mentioned in the *Plantae Novae Hispaniae*,[10] and apparently the collectors did not find it in their Mexican travels. Grisebach[11] says nothing of its occurrence in continental America, and, as late as 1887, Hemsley,[12] in the *Biologia Centrali-Americana*, knew but a single locality for the species on the continent of North America. The earliest con-

[5] A Voyage to the islands Madera . . . Jamaica, with the natural history, etc. **1**: 158. t. 101. f. 2. London, 1707.

[6] Fl. Jamaica **7**: 139. 1936.

[7] HBK. Nov. Gen. & Spec. **3**: 309. 1819.

[8] Flora of the Isthmus of Panama; in *The Botany of the Voyage of H.M.S. Herald*, pp. 57–254. 1854.

[9] Prodr. Syst. Nat. Regni Veg. **7**: 413. 1839.

[10] Plantae Novae Hispaniae. 1–184, i–xiii. Mexico, 1887.

[11] Flora of the British West Indian Islands. i–xvi, 1–789. London, 1864.

[12] Biologia Centrali-Americana **4**: 103. 1887.

tinental collections that I have seen are those of Rugel (1842 to 1849) from Florida, and of Schott (1864 and 1865) from Merida, Yucatan. It seems probable that the major portion of its spread in range has been in the last hundred years or less.

This plant was known to the early botanical explorers of the West Indies, and excited considerable interest because of its poisonous properties. It was described as *Lobelia longiflora* by Linnaeus and was subsequently transferred to *Isotoma* by Presl. Subsequent authors have followed Presl for the most part, but such a stand appears indefensible. *Isotoma*, as originally delimited, was a small Australian group, the species of which are scarcely separable generically from the African *Laurentia*. The transfer of the West Indian species to *Isotoma* was made because of the single character of the subequal corolla-lobes, a character that was emphasized in the original description of *Isotoma*. A glance at material of almost any of the Australian Isotomas, however, will make clear that the generic name is, in a sense, a misnomer; the lobelioid character of the corolla is plainly evident, with two small lobes opposed to three broader ones.

Linnaeus' *Lobelia longiflora* bears ample evidence of its relationship to the majority of endemic Lobelioideae of the West Indies. Its seeds bear close resemblance to those of many other species. The conspicuous free rim of the hypanthium simulates that found in many West Indian Lobelias, as do the bracteoles of the pedicel and the whole aspect of the calyx and capsule. The corolla, on the other hand, is unlike that of any other known species in America, but is closely similar to that of *Brighamia*, which is confined to the Hawaiian Islands.

The species is clearly marked, distinct from all other known species by the following combination of characters: Corolla white, salverform, the tube very long in proportion to its diameter, the lobes subequal; pedicels bracteolate; free rim of the calyx surpassing the ovary, which is nearly wholly inferior; seeds foveolate-reticulate. It appears reasonable to regard this as the only species of a distinct genus, quite apart from "*Laurentia*," "*Isotoma*," and *Lobelia*. The earliest available name for such a genus appears to be that proposed by Don. According to Dalla Torre and Harms (Gen. Siph. 521. 1900–1907) this name is antedated by *Stooria* (Neck., Elem. 1: 131. 1790). Necker's genera are so poorly characterized, however, that it is impossible to determine their identities.

2. DIASTATEA Scheidweiler, Allg. Gartenz. 9: 396. 1841.

TYPE SPECIES: *Diastatea virgata* Scheidw., *l.c.*

Stems erect, simple or with from few to many ascending subordinate lateral branches from the basal half. Plants annual, with branched fibrous roots. Leaves cauline, membranaceous or chartaceous in dried material, the

upper and middle ones largest and acutely pointed, the lower ones decreasing in size downward and the lowest often obtuse or rounded.

Inflorescences racemose, terminal on the branches, the central one usually much exceeding the others, if any. Racemes simple, slightly to strongly secund, loosely flowered (flowers usually 1 cm. apart on the axis, or more than this). Pedicels filiform, spreading-ascending, often upcurved or bent distally so that the mature capsule is erect or nearly so, ebracteolate. Flower-bracts foliaceous, the lowest similar to the upper leaves in size and shape, the upper narrower, the uppermost linear.

Hypanthium in anthesis broadly cupshaped, varying to flattish or to obconic, glabrous or roughened at base, much exceeded by the ovary, in fruit nearly unchanged or becoming obconic or turbinate. Capsule superior or nearly so, inclosed by the stretched persistent corolla, not more than $\frac{1}{3}$ of its length contained in the hypanthium (rarely nearly $\frac{1}{2}$ its length in exceptional individuals of *D. tenera*), bilocular, dehiscing loculicidally by apical valves. Placentae axile.

Flower inverted in anthesis. Corolla glabrous, purplish-blue. Tube in anthesis narrowly cylindric (except in *D. expansa*), entire, not slit dorsally, the dorsal sinus about as deep as the lateral ones. Tube much stretched by the expanding capsule and becoming at length scarious and hyaline. "Upper" lobes (the two opposite the three larger anthers) oblanceolate or with an elliptic blade and a long claw, mostly with an expanded deltoid base. The three "lower" lobes fused into a distinct lip, this more or less abruptly deflexed and bituberculate at base.

Filaments equalling or slightly exceeding the corolla-tube, connate a part of their length above, below free from each other and loosely adherent to the corolla-tube. Anther-tube bluish gray, two of the anthers shorter than the others and minutely white-tufted at tip; three larger anthers mostly glabrous.

Seeds many, light-brown, ellipsoid, smooth and shining, 0.5–0.6 mm. in length.

There are in this genus six well-defined entities, of which three are here described as new. The genus is characterized by the almost superior ovary and capsule, and by the long-persistent corolla which is much distended by the developing ovary and becomes at length hyaline. The group as a whole is closely akin to some Mexican species of *Lobelia*, and is, indeed, separable from these by arbitrary characters only. *L. sublibera*, a montane species of Tamaulipas and Nuevo Leon, has capsule and corolla characters almost identical with those of the species of *Diastatea*, the one exception being the corolla-tube which in *L. sublibera* is slit nearly to the base. The same thing is found to a lesser extent in *Lobelia xalapensis*, a wide-spread species of tropical America; in this species the capsule is about one-third inferior, and the corolla is somewhat enlarged and persistent. *Lobelia Dielsiana*, a local but perfectly distinct species of southwestern Mexico, not only has the superior ovary and the corolla of *Diastatea*, but has the corolla-tube slit not more than two-thirds its length.

The earliest available name for such a genus appears to be *Diastatea*, proposed by Scheidweiler in 1841. The single species described, *D. virgata*, was said to grow in "Mejico." Scheidweiler's original material has not been located, but his description can apply to no species except the one subsequently described as *Lobelia ramosissima* Mart. & Gal. The descriptions of *Diastatea* and of *D. virgata* are reprinted below, with the critical or diagnostic phrases italicized:

"DIASTATEA *mihi. Calycis tubo subnullo*, limbo quinquepartito; corolla fauci calycis inserta, *tubo longissimo integro*, limbo bilabiato, laciniis superioribus angustioribus; stamina 5 cum corolla inserta, filamenta libera, glabra, antherae in tubum connatae, superiores dorso hispidae, inferiores biaristatae, aristae inaequales. *Ovarium sessile, liberum, cylindricum;* stylus et stigma Lobeliae; *capsula bilocularis, supera, libera, tubo corollae inclusa*; semina indefinita.

"DIASTATEA *virgata*. Planta perennis ? ramosissima, ramis virgatis; *foliis inferioribus ovatis, superioribus lanceolatis, omnibus incisodentatis*, acutis, apice integerrimis, decurrentibus, caule ramulisque glabris; pedunculis axillaribus solitariis, filiformibus, *calycis laciniis subulatis utrinque margine uni-biglandulosis*, glandulis stipitatis; corollae limbi laciniis mucronulatis; flores coerulei."

Scheidweiler was so much impressed by the differences between his plant and the species of *Lobelia* known to him that he went on to emphasize the generic characters of *Diastatea* in German: " . . . der Fruchtknoten in der Mitte des Fruchtbodens ist ganz frei, ausser allem Zusammenhange mit dem Kelche; die Kapsel ist ebenfalls frei, und bleibt nach der Reife von der Kronenröhre umhüllt."

Diastatea as a whole appears to be somewhat more highly evolved than the genus *Lobelia*. The annual duration of all the species points to this, as do the characters of the nearly superior ovary, the ebracteolate pedicels, the peculiarly formed corolla, and the distribution, which is centered in Central America and southern Mexico.

KEY TO THE SPECIES

1. Corolla-tube 4.0–4.5 mm. long, narrowest at base and much enlarged distally; filaments 4.0–4.5 mm. long; middle and upper leaves lanceolate or narrowly elliptic, 4–8 times as long as wide, 0.3–0.4 cm. wide ..... 1. *D. expansa*

1. Corolla-tube (in anthesis, before swollen by the expanding capsule) linear, narrowly cylindric, not at all enlarged distally 2

2. Middle cauline leaves linear or narrowly elliptic, 0.1–0.25 cm. wide; filaments 6.0–7.5 mm. long (rarely 5.0–9.0 mm.); calyx-lobes glabrous, entire or toothed, 1.0–3.5 mm. long ..... 4. *D. tenera*

2. Middle cauline leaves linear-lanceolate or broader, 0.3–4.0 cm. wide; if less than 1 cm. wide, the filaments 3.0–4.8 mm. long 3

3. Filaments 3.0–4.8 mm. long; flower, including hypanthium, 4.5–10.0 mm. long 4

4. Calyx-lobes strongly prickly-ciliate on margins, 0.5–1.0 mm. wide at base, 4.0–6.0 mm. long; pedicel usually plainly scabrous under a lens; capsule 2.5–3.5 mm. in diameter; flower-bracts linear or nearly so, mostly strongly appressed to the stem. Pubescence mostly confined to the wing-like angles of the stem ..... 3. *D. costaricensis*

4. Calyx-lobes glabrous or sparingly ciliate, rarely as much as 0.5 mm. wide at base, 1.5–3.5 (rarely 5.5) mm. long; pedicel smooth and glabrous; capsule 1.5–2.5 mm. in diameter, flower bracts not appressed, the lower lanceolate or broader. Pubescence evenly distributed around the terete or angled stem. 2. *D. micrantha*

3. Filaments 7.5–11.0 mm. long; flower, including hypanthium, 12–22 mm. long 5
5. Calyx-lobes entire but closely and prominently ciliate on margins; pedicels prickly-ciliate under a lens; stem terete or angled, not winged, pubescent below with evenly distributed soft hairs ..... 5a. *D. virgata* var. *ciliata*

5. Calyx-lobes glabrous but with minute teeth on margins; pedicels smooth and glabrous; stem winged from the decurrent leaf-bases, with stiffish hairs on the margins of wings and few if any elsewhere ..... 5. *D. virgata*

1. **Diastatea expansa** McVaugh, sp. nov. Corollae tubo infundibuliforme, basi plus minusve gibboso, 4.0–4.5 mm. longo; filamentis 4.0–4.5 mm. longis; lobis calycis glabris, minute dentatis, 2.5–3.5 mm. longis; foliis mediis superioribusque ellipticis lanceolatisve, inferioribus latioribus.

Type locality: Correra, Dist. Temascaltepec, Estado de Mexico, at 1230 meters elevation. TYPE, *G. B. Hinton 2644*, Nov. 19, 1932, in the Gray Herbarium.

Stems simple or with a few weak side branches, slender (1 mm. in diameter at base), purplish below, 20–25 cm. high, glabrous, minutely scabrous on the somewhat winged angles. Leaves 8–14, thin, glabrous, spreading or somewhat appressed, the middle and upper ones elliptic or lanceolate, acute at tip, acute or rounded at base, sessile, 0.3–0.4 cm. wide by 1.3–2.5 cm. long, the margins finely and regularly serrate with 5–7 prominent teeth per cm. Lower leaves smaller and relatively broader, the lowest obtuse, suborbicular, subpetiolate, about 0.3 by 0.3 cm.

Inflorescence weakly secund, from few- to 11-flowered, few to 11 cm. long. Pedicels laxly ascending (in flower), to 11 mm. long in flower, smooth and glabrous. Flower-bracts leafy (except sometimes the uppermost), elliptic or lanceolate to linear, the lower ones 0.4–0.5 cm. wide by 1.8–2.5 cm. long.

Hypanthium glabrous, 1 mm. long or less. Ovary fusiform, 3 mm. long in anthesis. Fruit not seen. Calyx-lobes linear-lanceolate, acute, glabrous with 1 or 2 minute teeth on each edge, 2.5–3.5 mm. long.

Flower 8.5–9.5 mm. long, including hypanthium. Corolla purplish-blue (when dried). Tube 4.0–4.5 mm. long, slightly gibbous at base on lower side (in line with the two smaller anthers), narrowest at base and gradually expanded distally. Two upper lobes oblanceolate, 1.0–1.3 mm. wide by 4.0–5.0 mm. long; lobes of the lower lip elliptic, 2.0–2.5 mm. wide by 4.0 mm. long. Filaments 4.0–4.5 mm. long. Anther-tube 1.3–1.5 mm. long.

Seeds not seen.

Known only from the type collection.

2. DIASTATEA MICRANTHA (HBK.) McVaugh, Bull. Torrey Club **67**: 143. 1940.

Lobelia micrantha HBK., Nov. Gen. & Sp. **3**: 316. 1819 (247 of folio ed.).

Type locality: Ecuador. ("in Regno Quitensi, prope pagum Puembo, alt. 1300 hex."). TYPE: not seen. ISOTYPE, in herb. Kunth, photographed in the herbarium of the Botanical Museum, Berlin (Field Mus. neg. 9110).

Lobelia subtilis HBK., *op. cit.* 317 (folio ed. 247), *ex char. Lobelia ruderalis* R. & S., Syst. **5**: 56. 1819, fide Kunth, HBK., *op. cit.* **3**: 455. 1820. *Lobelia Draba* R. & S., Syst. **5**: 67. 1819, fide Kunth, *l.c. Rapuntium micranthum* Presl, Prodr. Mon. Lob. 25. 1836. *Rapuntium subtile* Presl, *l.c. Lobelia parviflora* Mart. & Gal., Bull. Acad. Brux. **9**: 41. 1842 (TYPE, *Galeotti 1970*, from Oaxaca, seen in the herbarium of the Jardin Botanique de l'État, Bruxelles). *Lobelia minutiflora* Kunze, Linnaea **16**: 318. 1842, *ex char. Laurentia ovatifolia* B. L. Robinson, Proc. Amer. Acad. **26**: 166. 1891 (TYPE, *Pringle 2985*, from Jalisco, seen in the Gray Herbarium). *Dortmannia micrantha, D. minutiflora* O. Ktze. Rev. Gen. Pl. **2**: 972. 1891. *Dortmannia parviflora* O. Ktze., *op. cit.* 973. *Laurentia micrantha* A. Zahlbr., Bull. Torrey Club **24**: 386. 1897, non A.DC. *Laurentia pedunculata* Brandg., Univ. Calif. Publ. Bot. **6**: 73. 1914 (TYPE, *Purpus 6705* from Chiapas, not seen. ISOTYPES, in Gray Herbarium and herbarium of the New York Botanical Garden, are *D. micrantha*). *Laurentia Maximiliana* E. Wimm., Rep. Sp. Nov. **38**: 78. 1935, *ex char. Laurentia micrantha* var. *longibracteata* E. Wimm., Rev. Sudamer. Bot. **2**: 104. 1935. *Laurentia micrantha* var. *ovatifolia* E. Wimm., Field Mus. Publ. Bot. **13**(6): 476. 1937. *Laurentia michoacana* var. *ovatifolia* B. L. Robinson, Proc. Amer. Acad. **26**: 167. 1891, nomen nudum. *Laurentia michoacana* B. L. Robinson, *l.c.*, nomen nudum. *Lobelia Turckheimii* Vatke, ex B. L. Robinson, *l.c.*, nomen nudum.

Stem simple or with many ascending branches, very slender to somewhat coarse (maximum size about 3 mm. in diameter at base), green, or purplish below, or sometimes purple throughout, from few to 50 (75) cm. high, chaffy-pubescent, especially below, or varying to practically glabrous; hairs, when present, nearly uniformly distributed around the terete or angled stem, flaccid and collapsed when dried. Plants exceedingly variable in size and pubescence. Leaves mostly about 10 on the main stem, the middle and upper ones lanceolate to ovate, acute at tip, narrowed to a margined petiole or a distinct slender petiole as much as 0.7 cm. long, less often the blades sessile. Lower leaves smaller, ovate to orbicular, mostly obtuse and petiolate. Texture of blades chartaceous or membranaceous. Pubescence, when present, mostly concentrated near margin, on veins of lower surface, and on upper surface near base. Margin variously serrate, the principal serrations mostly sharp, 5–6 per cm., but the margin sometimes sinuate or coarsely jagged-toothed, or minutely serrulate with as many as 12 teeth per cm. Size of blades ranging up to 2.2 by 5.5 cm., these usually 1 to 2 times as long as broad. Petioles ranging from 0.3 to 1.3 cm. in length.

Inflorescences often somewhat secund, the principal one from few- to 25-(30-) flowered, from few to 25 (30) cm. in length. Pedicels 6–27 (42) mm. long in fruit, the distal end often upcurved in fruit, smooth and glabrous (less often ciliate or chaffy-hirsute). Lower flower-bracts lanceolate, resembling reduced leaves; upper bracts narrower, linear to filiform, toothed. Lower bracts 0.2–1.5 by 1.0–3.5 cm.; upper ones 0.3–1.5 cm. long.

Hypanthium mostly glabrous, in fruit becoming conic, slightly higher than broad, 0.5–1.0 mm. high. Capsule narrowly ellipsoid, 1.5–2.5 mm. in

diameter by 3.0–6.0 (8.0) mm. long (average size 2 by 5 mm.). Calyx-lobes linear, usually less than 0.5 mm. in width at base, acute to acuminate at tip, entire or ciliate-toothed, 1.5–3.5 (5.5) mm. long.

Flower 4.5–6.5 (8.0) mm. long, including hypanthium. Corolla dark purplish-blue to pale lilac, pale blue or white. Tube 2.5–4.0 mm. long. Two upper lobes broadly triangular, about 1.5 mm. long; lobes of the lower lip rounded-spatulate, about 1 mm. broad by 2.0 mm. long. Filament-tube (3.0) 3.5–4.0 (4.5) mm. long. Anther-tube (0.5) 0.7–1.1 (1.3) mm. long, the three larger anthers glabrous or somewhat pubescent.

Seeds about 0.5 mm. in length.

Well-drained situations; fields, pastures and roadsides, limestone ledges, thickets, pine forests, open hillsides and barrancas. Highlands of San Luis Potosí to Vera Cruz and Jalisco, south throughout the highlands of southern Mexico and Central America; in the Andes to Peru and Bolivia. Occurs mostly at elevations of 1,000 to 2,700 meters. Flower and fruit nearly throughout the year.

Diastatea micrantha is the most variable and the most widely distributed species of the genus. It ranges from San Luis Potosí to Bolivia and the many variations appear to be distributed throughout, without geographic segregation.

3. **Diastatea costaricensis** McVaugh, sp. nov. *D. micranthae* similis; marginibus loborum calycis valde echinato-ciliatis, lobis 4.0–6.0 mm. longis, basi 0.5–1.0 mm. latis, pedicellis sub lente scabris; capsulis diametro 2.5–3.5 mm.; bracteis sublinearibus, appressis; caulibus plus minusve alatis, alis ciliatis.

Type locality: near San José, Costa Rica. TYPE: *Oersted 9238*, November 1846, in the herbarium of the Universitetets Botaniske Museum, Copenhagen.

Laurentia irazuensis Wimmer in Standl., Field Mus. Publ. Bot. **18**(4): 1415. 1938, non *Lobelia irasuensis* Pl. & Oerst., 1857.

Stem simple or with few to many ascending branches, 0.5–2.0 mm. in diameter at base, usually purplish at least at base, few to 34 cm. high, usually somewhat wing-angled below the decurrent leaf-bases. Pubescence of subrigid chaffy hairs, mostly confined to the wing-angles of the stem, especially the basal portion; some of the hairs, at least the shortest ones, usually remaining erect and not collapsed in dried specimens. Leaves mostly about 10 on the main stem, papery, somewhat appressed, the middle and upper ones lanceolate to linear-lanceolate, acute or acuminate at tip, narrowed to a sessile cuneate base. Lower leaves smaller and relatively broader, acute or obtuse at tip, sessile or subpetiolate. Pubescence mostly confined to the margin, the veins of the lower surface, and the base of the blade on the upper surface. Margin finely but somewhat irregularly serrate with 4–8 teeth per cm. Blades 0.3–0.6 cm. wide by 1.0–2.5 cm. long; blades of lowest leaves as small as 0.2 by 0.3 cm.; upper and middle blades mostly 3–4.5 (6.0) times as long as wide.

Inflorescences usually plainly secund, the principal one 5–16 cm. in length, from few- to 13-flowered. Pedicels 4–16 mm. long in fruit, the distal end usually strongly upcurved in fruit, so that the capsule is erect, usually plainly scabrous under a lens. Flower-bracts narrowly elliptic to linear, the lower resembling reduced leaves, all appressed to the axis, usually strongly so; size (of lower bracts) 0.2–0.4 by 1.0–2.7 cm.

Hypanthium glabrous, in fruit about as broad as high, 0.8–1.1 mm. high. Capsule broadly ellipsoid, 2.5–3.0 mm. in diameter by 5.0–6.5 mm. long. Calyx-lobes narrowly triangular, usually plainly tapering from base to apex, 0.5–1.0 mm. wide at base, strongly prickly-ciliate on margins, 4.0–6.0 mm. long.

Flower 5.0–7.0 mm. long, including hypanthium. Corolla blue-purple. Tube 3.0–4.0 mm. long. Two upper lobes broadly triangular, 1.3–1.5 mm. long; lobes of the lower lip rounded-spatulate, about 1 mm. broad by 1.5 mm. long. Filaments 3.5–4.0 mm. long. Anther-tube 0.9–1.1 mm. long, the three larger anthers minutely pubescent.

Seeds about 0.5 mm. in length.

Grassy hillsides, pastures, roadside ditches. Guatemala to Costa Rica, at elevations of 800 to 1,800 meters. Flowering and fruiting from November to February (according to specimens seen).

Specimens examined:[13] GUATEMALA: without locality, *E. T. Heyde 381* and *537* (US); SANTA ROSA: Estanzuela, *Heyde & Lux, J. D. Sm. Pl. Guat. 4257* (G, NB, US); "in collib. herbid., Guatemala, Cerro del Carmen," *Bernouilli 146* (NB). COSTA RICA: Bords du Rio Torres près de San Francisco de Guadalupe, *Tonduz 7230* (US); San José, etc., *Tonduz 1414* (US); San Sebastian, Prov. San José, *Standley 32717* (US); Santa Marta de Dota, Prov. San José, *Standley 41587* (F); San Ramon, *A. M. Brenes 3777, 4752, 5300, 5860a, 16851* (F); prope San José, *Oersted 9238*, Nov. 1846 (Cop); Segovia, *Oersted 9244*, Jan. 1848 (Cop). HONDURAS—COMAYAGUA: vicinity of Siguatepeque, *Standley 55995* (F, US).

This species was first collected by Oersted in Costa Rica in 1846. It was later described by Planchon and Oersted under *Lobelia parviflora* "As far as one can judge from the short diagnosis of *Lobelia parviflora*, our material belongs to that species. It grows in meadows at San José, Costa Rica (4,000 ft. alt.), and at the same height in Segovia at Xinoteca; with flower and fruit in December and January." Wimmer later mistakenly identified the Oersted material of *Diastatea costaricensis* as *Lobelia irasuensis* Pl. & Oerst., which is a true *Lobelia* and not even closely related to the present species; the original description of *L. irasuensis* is carefully drawn, and the type, *Oersted 9246*, collected at 8,000 feet on Mt. Irazu, is preserved in the herbarium of the Universitetets Botaniske Museum, Copenhagen.

When *Diastatea costaricensis* grows in and about the same localities where *D. micrantha* is found, it is always easily separable from it. No true

[13] See list of abbreviations for herbaria at end of paper.

intermediates have been seen, although occasional specimens show intergradation in one or two characters.

4. DIASTATEA TENERA (A. Gray) McVaugh, Bull. Torrey Club **67**: 143. 1940.

Palmerella tenera A. Gray, Proc. Amer. Acad. **22**: 433. 1887. Type locality: Rio Blanco, Jalisco. TYPE: *E. Palmer 552*, Sept. 1886, in the Gray Herbarium. *Lobelia Palmeri* Greene, Pittonia **1**: 297. 1889. *Laurentia pinetorum* Brandg., Univ. Cal. Publ. Bot. **4**: 92. 1910. TYPE, *Purpus 3665*, from Popocatapetl, not seen. ISOTYPES, in Field Museum, Gray Herbarium and New York Botanical Garden, are *D. tenera*.

Stem simple or with few subordinate side branches from the lower part, slender, usually not exceeding 1 mm. in diameter at base, purplish at least below, from few to 30 (64) cm. high, glabrous or minutely scabrous-puberulent, scabrous below on the angles. Leaves usually 6–8, thin, glabrous, somewhat appressed, the middle and upper ones linear or narrowly elliptic, acute at both ends, sessile, 0.1–0.25 cm. wide by 0.8–3.5 cm. long, the margins finely and shallowly serrulate with about 4 teeth per cm. Lower leaves smaller and relatively broader, obtuse or acute, mostly 0.2–0.4 cm. wide by 0.3–0.8 cm. long, sessile, or less often subpetiolate.

Inflorescence usually strongly secund, from few to 15 (32) cm. long, loosely from 1- to 10- (20-) flowered. Pedicels usually arcuate (sometimes abruptly upcurved near tip) so that the mature capsule is erect or nearly so, often somewhat thickened beneath the hypanthium and merging imperceptibly with it, 6.0–20.0 (48.0) mm. long, smooth and glabrous. Flowerbracts (except occasionally the lowest) linear, resembling reduced leaves, 1.0–2.0 mm. wide by 5.0–15.0 (20.0) mm. long.

Hypanthium usually oblique, glabrous, becoming conic or turbinate in fruit, as long as or longer than broad, 1.0–1.5 (3.0) mm. high. Capsule 1.5–2.5 (3.5) mm. in diameter by 5.0–7.0 (8.0) mm. long. Calyx-lobes linear to elliptic or lanceolate, acute at tip, glabrous, with 1 or 2 minute teeth on each edge or less often entire, (1.0) 1.5–3.0 (3.5) mm. long.

Flower 10–16 mm. long, including hypanthium. Corolla purplish-blue ("purple," or "deep lilac"), with white or yellowish eye, the lower lip bituberculate at base. Tube narrowly cylindrical, not expanded above, (the lobes flaring abruptly) slightly gibbous at base on lower side, (in line with the two shorter anthers) 5.0–7.5 (8.0) mm. long. Two upper lobes linear-spatulate, 1.0–1.5 mm. wide by 3.5–5.0 mm. long; lobes of the lower lip obovate, rounded or truncate at tip, mucronate, 1.5–2.5 (4.0) mm. wide by 4.0–7.0 mm. long. Filaments (5.0) 6.0–7.5 (9.0) mm. long. Anther-tube (0.8) 1.0–1.3 (1.5) mm. long, the three larger anthers minutely puberulent or glabrous.

Seeds about 0.5 mm. in length.

Pine forests, streamsides, damp grassy glades, barrancas, moist meadows and mountainsides, at elevations of 1,400 to 2,600 meters. Jalisco to Puebla and Guerrero.

Specimens examined: MEXICO—GUERRERO: Petlacala, *Mexia 8959* (USNA). JALISCO: Sierra de San Esteban, *Pringle 8756* (ANS, F, G, NB,

US); near Guadalajara, *Rose & Painter 7474* (G, US); near Guadalajara, *Pringle 2374* (ANS, G, NB), *Pringle 2163* (F, G); Rio Blanco, *Dr. Edw. Palmer 552* (ANS, G, TYPE; NB); San Sebastian, e. of Arroyo del Cura, *Mexia 1378* (NB, US); Road to San Domingo Mine, Etzatlan, *Barnes & Land 319* (F). MEXICO (Estado de): Tultenango, *Pringle 3527* (G); near Tultenango, *Rose & Painter 7842* (G, US); Dist. Temascaltepec, Carboneras, *Hinton 2122* (NB), Volcan, *Hinton 2507* (NB), *Hinton 2211* (NB), Communidad, *Hinton 2457* (G). MICHOACAN: Cerros San Miguel, *Bro. G. Arsene 6070* (NB, US), *6064* (NB, US), *5565, 6539, 6542* (US); La Huerta, *Bro. G. Arsene 5979* (US); Loma Santa Maria, *Bro. G. Arsene 3113* (US), *5865* (G, US). MORELOS: near Cuernavaca, *Pringle 7058* (G); mountainside above Cuernavaca, *Pringle 15028* (G). PUEBLA: Tepoxuchil, near Puebla, *Bro. Nicolas* (G, US); Manzanilla, *Bro. G. Arsene 2373* (US); Laguna de San Baltasar, *Bro. G. Arsene 57* (US); pres l'Hacienda Alamos, route de Veracruz, *Arsene 7073* (US); Fort la Guadalupe, *Arsene 269* (US); STATE UNKNOWN: Popocatepetl, *C. A. Purpus 3665* (F, G, NB).

D. tenera is more variable in flower-size than is usual in this genus, but all the material seen appears to be sufficiently uniform in character to justify its inclusion in a single species.

5. DIASTATEA VIRGATA Scheidw., Allg. Gartenz. **9**: 396. 1841. Type locality: Mexico. TYPE: not seen.

Lobelia ramosissima Mart. & Gal., Bull. Acad. Brux. **9**: 42. 1842. Type locality "cordillere orientale d'Oaxaca." TYPE: *Galeotti 1971*, in the herbarium of the Jardin Botanique de l'État, Bruxelles. *Laurentia ramosissima* Benth. & Hook. f., ex Hemsley in Biol. Cent. Am. Bot. **2**: 265. 1881.

Stems simple or with few to many branches, sometimes with much-branched bushy habit; branches strongly ascending. Stems green or purplish at base, sometimes more than 2.5 mm. in diameter at base, from 15 to more than 45 cm. high, conspicuously winged from the decurrent leaf bases, the wings chaffy-pubescent with stiffish hairs, especially on the lower parts of the stem. Leaves thin and papery, glabrous or sparsely hispid near the base and on margin, from few to 10, spreading, coarsely incised-dentate; size (of leaves at base of inflorescence) 1.3 × 4.3 cm.; middle cauline leaves 1.5–2.5 cm. broad by 2.5–6.0 cm. long; shape elliptic to lance-ovate (lower "ovate-subrhomboid" according to Mart. & Gal.), or the upper ones narrowly lanceolate to linear, merging into the flower-bracts. Tip blunt-pointed, mucronulate. Base cuneate, sessile or subpetiolate, or the lowest leaves with a petiole to 0.8 cm. long, and the base rounded.

Inflorescence secund, 15–30 cm. long, loosely from 10- to 25-flowered. Pedicels smooth, often arcuate, strongly ascending or the lowest widely spreading, 12–30 (55) mm. long in fruit. Flower-bracts linear or the lower broader, leafy; middle and upper ones usually about 1.0 cm. long.

Hypanthium in anthesis about 1 mm. long, glabrous, in fruit about the same size. Capsule 2.0–2.5 mm. in diameter by 9.0–13.0 mm. long, elliptic to linear, often slightly curved. Calyx-lobes narrowly linear, acutely pointed, 2.5–6.5 mm. long, minutely callose-denticulate on margins.

Flower 17–22 mm. long, including hypanthium. Corolla "bleu," the tube 8–11 mm. long, in anthesis narrowly linear, about 1 mm. in diameter. Lobes

of the lower lip spreading, deflexed, obovate or elliptic, 2.5–3.5 mm. broad by 6.0–8.5 mm. long. Two upper lobes linear to elliptic-oblanceolate, usually clawed, 1.5–2.0 mm. wide by 4.0–6.0 mm. long. Filament-tube 8.0–11.0 mm. long, the filaments shortly connate above. Anther-tube 1.6–2.0 mm. long.

Seeds about 0.6 mm. in length.

Mountains of Oaxaca and (?) Vera Cruz, at elevations of 1,000 to 2,000 meters. Collected in flower and fruit from November to February.

Specimens examined: MEXICO—OAXACA: Yavezia, *Galeotti 1971* (Brux, TYPE; US); Jayacatlan, *L. C. Smith 284* (G); Monte Alban, near Oaxaca City, *Chas. L. Smith 721* (NB, US); El Parian, Etla, *Conzatti & Gonzalez 904* (G); La Hoya Canyon, *Pringle 5887* (G); Santa Catarina, *Conzatti 1665* (F). VERA CRUZ: "Cordillera, Vera Cruz," 3,000 ft., *H. Galeotti*, fevrier (1840?) (US).

5a. DIASTATEA VIRGATA Scheidw., var. **ciliata** McVaugh, var. nov. *D. virgatae* similis; lobis calycis integris, valde ciliatis; caulibus teretibus vel angulatis, non alatis, ubique pubescentibus; pedicellis sub lente scabris; foliis mediis late ovatis, acute serratis, non incisis.

Type locality: Mountains above Iguala, Guerrero. TYPE: *Pringle 8375*, in the Gray Herbarium.

Habit essentially that of *D. virgata*. Stem terete or angled, not winged, chaffy-pubescent, especially below, with soft hairs which are more or less evenly distributed. Height 12–52 cm. Leaves thin and papery, about 10, sparsely pubescent on the veins below and on the upper surface and margin. Middle and upper leaves broadly ovate, acute at tip, rounded at base and narrowed abruptly into a margined petiole 1.0–5.0 mm. long, the blades 2.0–4.0 cm. wide by 2.5–6.0 cm. long. Margins irregularly and usually sharply serrate with 4–8 teeth per cm. Lower leaves smaller, the lowest often rounded and obtuse, petiolate.

Inflorescence secund, 9–17 cm. long, loosely from 10- to 16-flowered. Pedicels usually abruptly upcurved distally in fruit, 10–15 mm. long, rough-ciliate. Lower flower bracts leafy, usually ovate, the upper lanceolate to linear.

Hypanthium roughened at base, little changed in fruit, becoming 1.0–1.2 mm. high. Capsule ellipsoid, 2.0–2.5 mm. in diameter by 8.0–11.0 mm. long. Calyx-lobes linear or very narrowly triangular, long-pointed, entire but closely and prominently ciliate on the margins, 4.5–6.5 mm. long.

Flower essentially as in *D. virgata*. Length 12–14 mm., including hypanthium. Corolla purplish-blue (when dried). Tube 7.0–8.5 mm. long. Two upper lobes 1.0–1.5 mm. broad by 3.0–4.0 mm. long; lobes of the lower lip 1.5–3.0 mm. broad by 3.5–5.0 mm. long. Filaments 7.5–8.5 mm. long. Anther-tube 1.2–2.0 mm. long.

Seeds as in *D. virgata*.

Limestone hills and ledges, mountains of southern Mexico at altitudes of 900 to 1,200 meters. Flower and fruit from September to November.

Specimens examined: MEXICO—GUERRERO: mountains above Iguala, *Pringle 8375* (ANS, F, G, TYPE; NB, P, R, US). MEXICO: Vigas, Dist.

Temascaltepec, *Hinton 2628* (G). MICHOACAN: Cerro Azul, Morelia, *Bro. Arsene*, Sept. 17, 1910 (F). MORELOS: near Yautepec, *Pringle 11005* (F, G, NB, US).

This variety is very similar to *D. virgata*, to which specimens of it have previously been referred. The two are easily separated, however, by the key-characters noted above, as well as by the leaves, which in *D. virgata* are narrower and more prominently toothed than in var. *ciliata*. Geographically, also, the two appear to be distinct, although relatively few collections have been made of either.

3. LOBELIA, section *Isotoma* R. Br., Prodr. Fl. Nov. Holl. 565. 1810.

Laurentia Micheli, Nov. Pl. Gen. 18. t. 14. 1729; Adanson, Fam. Pl. **2**: 134. 1763. *Isotoma* Lindl., Bot. Reg. 964. 1826. *Palmerella* A. Gray, Proc. Amer. Acad. **11**: 80. 1876.

Ours perennial herbs with sessile leaves. Inflorescence a simple terminal raceme. Hypanthium in anthesis campanulate, the ovary inferior or essentially so. Placentation axile. Capsule bilocular, opening by apical loculicidal valves. Flower inverted in anthesis. Corolla strongly zygomorphic, the two (apparently) upper lobes narrower than the three lower ones, which are fused at base into a definite lip. Corolla-tube entire at apex, not cleft more deeply on the (apparently) upper side than between the upper and lower lips. Filaments united into a tube, at least distally. Anthers united into a tube, the two shorter ones white-tufted at apex and usually with short horn-like processes in addition. Seeds smooth, numerous.

A single species in North America, *Lobelia Dunnii* Greene.

KEY TO THE VARIETIES

1. Middle and upper leaves elliptic or lanceolate, 7.0–20.0 mm. wide; lower leaves obovate to oblanceolate, 9.0–30.0 mm. wide; plants usually bristly-pubescent at least in the inflorescence or, if glabrous, at least the corolla-tube pubescent ..1a. *L. Dunnii* var. *serrata*

1. Middle and upper leaves linear or narrowly elliptic, 2.5–9.0 mm. wide; lower leaves oblanceolate, 5–12 mm. wide; plants usually entirely glabrous or sparsely bristly. ..... 1. *L. Dunnii* var. *Dunnii*

1. LOBELIA DUNNII Greene, var. **Dunnii** McVaugh, nom. nov.

Lobelia Dunnii Greene, Pittonia **1**: 297. 1889. Based on *Palmerella debilis*. *Palmerella debilis* A. Gray, Proc. Amer. Acad. **11**: 80. 1876. Type locality: "Great Canyon of the Tantillas Mts., near the northern borders of Lower California." TYPE: *E. Palmer*, in 1875, in the Gray Herbarium. *Laurentia debilis* McVaugh, Bull. Torrey Club **67**: 144. 1940, non *Lobelia debilis* L. f., 1781.

This variety differs from the more widespread var. *serrata* as follows:

Pubescence none, or sparse and confined to the inflorescence (corolla always pubescent). Cauline leaves narrower than in var. *serrata*, the middle and upper ones linear or narrowly elliptic, 0.25–0.9 cm. wide by 4.5–11.0 cm. long, mostly 10–20 times as long as wide; lower leaves oblanceolate, 0.5–1.2 cm. wide by 2.0–5.0 cm. long, mostly 3–6 times as long as wide. Serration

often inconspicuous except on the lowest leaves, the middle and upper ones with essentially entire margins lined with minute callose teeth.

Pedicels 4–9 mm. long, smooth and glabrous (rarely somewhat prickly). Bracts as in var. *serrata* but narrower, in proportion to the leaves. Hypanthium usually glabrous; calyx-lobes glabrous or nearly so, 5–8 mm. long.

Flower 22–30 mm. long, including hypanthium. Corolla-tube 12–18 mm. long. Filaments 12–17 mm. long. Anther-tube 2.0–2.5 mm. long, glabrous or with a few hairs, the two shorter anthers tufted as in var. *serrata*.

Habitat of var. *serrata;* also "dry hillsides" and "moist meadows"; mountains of Baja California, at elevations up to 2,200 meters. Collected in flower and fruit from August 1 to October 1.

Specimens examined: MEXICO—BAJA CALIFORNIA: "Tantillas Canyon, S. Diego Co.," *Edw. Palmer*, anno 1875 (G, TYPE); "Big Canyon, Tantillas Mts., s. part of San Diego Co.," *Edw. Palmer 210*, anno 1875 (F, NB); Big Canyon, *Geo. W. Dunn*, Sept. 20, 1881 (Cath, NB); Rancho San José, foot of Sierra San Pedro Martir, east of San Telmo, *Wiggins & Demaree 4814* (F, G, NB, P, US); Canyon Cantiles, *C. R. Orcutt*, Aug. 1, 1883 (F, G, US); La Sanca, Sierra San Pedro Martir, *Wiggins & Demaree 4861* (G, NB, P); La Encantada, Sierra San Pedro Martir, *Wiggins & Demaree 4996* (F, G, NB, P).

The nomenclatorial type of this species is a plant which has as yet not been found except in Baja California, where it was first collected by Dr. Edward Palmer in 1875. The far better-known variety *serrata* was discovered in California the same year.

1a. LOBELIA DUNNII Greene, var. **serrata** (A. Gray) McVaugh, comb. nov. *Palmerella debilis* var. *serrata* A. Gray, Bot. Calif. **1**: 619. 1876. Type locality: "Valley of Ojai Creek, Ventura Co." (California). TYPE: *Rothrock 173*, in the Gray Herbarium. Isotypes seen in various herbaria. *Lobelia Rothrockii* Greene, Pittonia **1**: 297. 1889. *Laurentia debilis* var. *serrata* McVaugh, Bull. Torrey Club **67**: 144. 1940.

Stem decumbent or erect, simple or with ascending subordinate lateral branches, rather coarse (maximum size about 4 mm. in diameter at base), light green (often straw-colored below in dried specimens), 20–85 cm. high, smooth and glabrous below the inflorescence or sometimes throughout. Cauline leaves 20–35, spreading, membranous, at least the middle and lower ones smooth and glabrous, the upper ones glabrous to short prickly-pubescent. Middle and upper leaves elliptic or lanceolate, acute at both ends, sessile, 0.7–1.5 (2.0) cm. wide by 3.5–9.5 cm. long, mostly 5–10 times as long as wide. Lower leaves shorter and broader, obovate to oblanceolate, acute at tip, narrowed at base into a broadly margined petiole, (0.9) 1.5–2.5 (3.0) cm. wide by 3.5–6.0 (9.0) cm. long, usually 2–4 times as long as wide. All leaves serrate, the lower coarsely so with sharp teeth, the upper shallowly so, with callose narrow teeth. Plants perennial.

Inflorescence often subcapitate, 2–7 (12) cm. long, densely few- to 23-flowered. Pedicels strongly ascending or the lower spreading, rather stout (to 0.6 mm. in diameter in fruit), (2.0) 4.0–8.0 (13.0) mm. long in fruit,

short bristly-pubescent to glabrous. Flower-bracts linear or the lower lanceolate or elliptic, resembling the upper leaves. Lower bracts attaining a size of 0.7 by 5.0 cm., but mostly about half this size; upper bracts linear, 2.0 cm. long or less.

Hypanthium in anthesis campanulate, mostly acute at base, bristly-pubescent to glabrous, campanulate to elliptic in fruit, 2.5–3.0 mm. in diameter. Capsule inferior or nearly so, 6–7 (12) mm. long. Calyx-lobes linear-subulate, with a short-deltoid base, entire, bristly-pubescent to glabrous, 6–14 mm. long.

Flower 20–25 mm. long, including hypanthium. Corolla-limb blue, the tube whitish (according to Jepson); both tube and limb pubescent, the former closely so within and less densely so without. Tube linear or nearly so, 9–12 (14) mm. long, at first entire, in age splitting incompletely on the dorsal side, split extending from near the base about half the length of the tube and exposing the dorsal filament. Lobes abruptly spreading from the summit of the tube, the two upper ones linear, acute, about 1 mm. wide by 5–7 mm. long; lobes of the lower lip fused at base, elliptic, 2.0–3.0 mm. wide by 6.0–8.0 (10.0) mm. long. Filaments 9.5–12.5 (14.0) mm. long, coherent into a tube above, free below nearly their whole length and loosely adherent to the corolla-tube, pubescent. Anther-tube 2.3–3.0 mm. long, bluish-gray, pilose with long white hairs, the two shorter anthers white-tufted at tip and sometimes with short straight hornlike processes in addition.

Seeds ellipsoid-lenticular, smooth and shining, light-brown, about 0.5 mm. in length.

Canyons and stream-beds, usually in moist soil, southern Coast-Ranges of California, from Monterey County to northern San Diego County and inland to the San Bernardino Mountains. Mountains, at elevations of 150 to 1,800 meters. Beginning to flower in June or early July; fruit August 1 to mid-October.

4. PORTERELLA Torrey, Hayd. Rep. Geol. Surv. Mont. 488. 1872.

Stems erect, simple or with few lateral branches, rarely diffuse and bushy, somewhat fleshy, very slender or stoutish, the maximum diameter at base about 4 mm. Color green. Entire plant smooth and glabrous, from few to 32 cm. high; plants occasionally with mature fruit when no more than 1.5 cm. high. Cauline leaves from few to 20, soft and lax, soon deciduous and often not persistent until flowering time, usually narrower than the flower-bracts. Blades sessile, entire or rarely sinuate in luxuriant specimens, linear-subulate or rarely lanceolate, 1.0–2.0 (4.0) mm. wide, (4.0) 10.0–20.0 (30.0) mm. long, the tip acute to acuminate or almost capillary. Plants annual, with slender fibrous roots; stem, in wet places, continued downward as an erect rootstock with roots at several nodes, plainly corky-parenchymatous below.

Inflorescence 6–20 cm. long (correspondingly less in dwarfed plants), loosely from 1- to 15- (25-) flowered. Pedicels spreading-ascending, slender (maximum diameter about 0.5 mm.), 5–20 (35) mm. long in fruit, expanded gradually into the base of the capsule, straight or arcuate. Flower-bracts linear to ovate, similar to the foliage leaves but usually broader and often longer than these, 1–4 mm. wide by 4–18 (27) mm. long, mostly 2.5–6.0 times as long as wide.

Hypanthium in anthesis narrowly obconic or turbinate, in fruit becoming turbinate or cylindric, long-acute and usually slightly oblique at base, (1.5) 2.0–3.0 mm. in diameter. Ovary inferior or essentially so. Placentation axile. Capsule bilocular, opening by apical loculicidal valves, (5.0) 7.0–10.0 (16.0) mm. long, wholly inferior or with 1–2 mm. of the tip not adherent to the hypanthium. Flower inverted in anthesis. Calyx-lobes linear, varying to narrowly triangular or elliptic, entire, rounded or acutish at tip, about 1.0 mm. wide (rarely as much as 2.5 mm.), 3–8 (11.0) mm. long.

Flower (9.0) 13.0–18.0 (20.0) mm. long, including hypanthium; odor said to resemble that of the cultivated heliotrope; corolla blue (rarely all white), with yellow or whitish eye and two folds at base of lower lip. Tube entire, linear or slightly enlarged distally, its long axis slightly oblique to that of the hypanthium, (3.5) 4.5–6.0 mm. long. Corolla strongly zygomorphic; two upper lobes erect, elliptic, 1.0–2.5 mm. wide, 3.5–5.5 mm. long; lobes of the lower lip elliptic or obovate, apiculate, 2–6 mm. wide, 4.5–9.0 mm. long. Filaments 3.0–6.0 (7.0) mm. long, coherent their whole length into a tube, free from the corolla. Anther-tube 1.5–2.6 mm. long, gray, all five anthers minutely white-tufted at tip, the two shorter ones plainly so, and with short horn-like processes in addition.

Seeds fusiform, light brown with minutely dark-apiculate tips, smooth and slightly lustrous, about 1 mm. long.

Marshes and wet meadows, margins of ponds, open muddy pools and ditches, growing in wet soil, often partially immersed; plants in partially dried mud are often dwarfed. Northwestern Wyoming to southeastern Oregon, south in the mountains to northern Utah, Coconino Co., Arizona, Elko Co., Nevada, and Tulare Co., California. Occurs principally at elevations of 1,500 to 3,000 meters. Flower and fruit mostly from June 15 to September 15.

A single species, with characters of the genus.

1. PORTERELLA CARNOSULA (Hook. & Arn.) Torr., *l.c.* (*P. carnulosa* Torr., *sphalm.*)

Lobelia carnosula Hook. & Arn., Bot. Beech. Voy. 362. 1840. Type locality: "Blackfoot River, Snake Country" (now southeastern Idaho). TYPE: Collected "by a friend of Mr. Tolmie" in 1837 and labelled "Tolmie"; now in the New York Botanical Garden. Sir J. Arthur Hill, who kindly instituted a search for the type of *Lobelia carnosula*, states that it is not to be found in the herbarium at Kew; the Tolmie plant at New York may therefore stand as the TYPE.

Laurentia carnosula Benth. & Hook. f., ex A. Gray, Bot. Calif. **1**: 444. 1876. *Porterella eximia* A. Nels., Bull. Torrey Club **27**: 270. 1900. Type locality: "Jackson's Lake, Uinta Co., Wyo." TYPE: *A. & E. Nelson 6544*, accession no. 20748 of the Rocky Mountain Herbarium of the University of Wyoming. *Laurentia eximia* A. Nels., New Man. Bot. Centr. Rocky Mts. 475. 1909.

In conclusion, the writer wishes to acknowledge his indebtedness to the curators of the several herbaria who have so kindly placed at his disposal

the collections in their charge. In citing exsiccatae, the following abbreviations are employed for herbaria:

ANS	Academy of Natural Sciences, Philadelphia, Pa.
Brux	Jardin Botanique de L'État, Bruxelles, Belgium.
Cath	Catholic University of America, Washington, D. C.
Cop	Universitetets Botaniske Museum, Copenhagen, Denmark.
F	Field Museum of Natural History, Chicago, Ill.
FS	Forest Service, U. S. Dept. of Agriculture, Washington, D. C.
G	Gray Herbarium of Harvard University, Cambridge, Mass.
Id	University of Idaho, Pocatello, Ida.
NB	New York Botanical Garden, New York, N. Y.
O	National Herbarium of Canada, Ottawa, Ont.
Ore	University of Oregon, Eugene, Ore.
P	Pomona College, Claremont, Calif.
R	Rocky Mountain Herbarium, Univ. of Wyoming, Laramie, Wyo.
US	United States National Herbarium, Washington, D. C.
USNA	United States National Arboretum, Washington, D. C.

Division of Plant Exploration and Introduction
Bureau of Plant Industry
United States Department of Agriculture

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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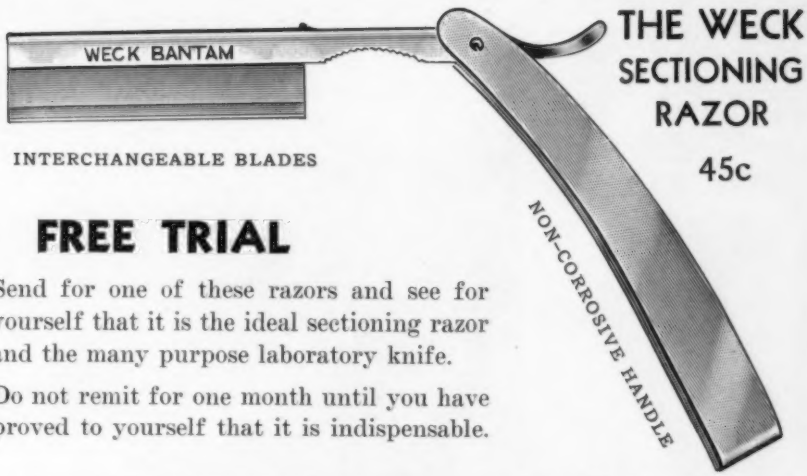

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